

# 28 Topics in the Evolution of Sexual Behavior in the Tephritidae

*John Sivinski, Martín Aluja, Gary Dodson, Amnon Freidberg, David Headrick, Kenneth Kaneshiro, and Peter Landolt*

## CONTENTS

28.1	Introduction .....	752
28.2	A Catalog of Sexual and Agonistic Behaviors.....	753
28.2.1	Mating Sites and Rhythms.....	753
28.2.1.1	The Influence of Resource Distribution on Mating Sites (J. Sivinski).....	753
28.2.1.2	Species Isolation and the Timing of Sexual Activity (M. Aluja).....	755
28.2.1.2.1	<i>Anastrepha</i> .....	755
28.2.1.2.2	<i>Toxotrypana</i> .....	755
28.2.1.2.3	<i>Bactrocera</i> .....	755
28.2.1.2.4	<i>Ceratitis</i> .....	756
28.2.1.2.5	<i>Rhagoletis</i> .....	756
28.2.2	Agonistic Behavior (G. Dodson) .....	756
28.2.3	Courtship .....	760
28.2.3.1	Acoustic Signals (J. Sivinski) .....	760
28.2.3.2	Visual Signals (J. Sivinski) .....	761
28.2.3.2.1	Color and Pattern.....	761
28.2.3.2.2	Ornaments .....	762
28.2.3.2.3	What Do Displays Mean? .....	762
28.2.3.3	Predation and the Evolution of Sexual Behavior (P. Landolt).....	764
28.2.3.3.1	Introduction.....	764
28.2.3.3.2	Predation and Sexual Signals .....	765
28.2.3.3.2.1	Visual Signals .....	765
28.2.3.3.2.2	Chemical Signals .....	765
28.2.3.3.2.3	Acoustic Signals .....	766
28.2.3.3.3	Predation and Encounter Sites .....	766
28.2.3.3.3.1	Resource-related Station Taking .....	766
28.2.3.3.3.2	Leks.....	766
28.2.3.3.3.3	Signaling .....	766
28.2.3.3.3.4	Mimicry .....	767
28.2.3.4	Trophallaxis (A. Freidberg).....	768
28.2.3.4.1	Introduction.....	768
28.2.3.4.2	Distribution in the Animal Kingdom .....	769
28.2.3.4.3	Distribution in the Tephritidae .....	769
28.2.3.4.4	Anatomy, Ultrastructure, and Biochemistry.....	771
28.2.3.4.5	Experiments .....	772
28.2.3.4.6	Evolutionary Implications and Phylogeny .....	772

28.2.3.5	Copulation Duration — Sperm Competition and Female Choice (M. Aluja).....	773
28.3	The Phyletic Distribution of Sexual Behaviors (D. Headrick) .....	773
28.4	Phylogeny and Behavior .....	780
28.4.1	Sexual Selection and Speciation (K. Kaneshiro) .....	780
28.4.2	Mating Behavior and the Reconstruction of Phylogeny (D. Headrick) .....	783
28.4.2.1	Homology and Homoplasy .....	783
28.4.2.2	Level of Taxonomic Analysis.....	785
28.4.2.3	Conclusion .....	785
	Acknowledgments .....	785
	References .....	786

## 28.1 INTRODUCTION

The sex lives of the Tephritidae are wonderfully various. They range in complexity from males that couple after little preliminary courtship signaling to those that produce a repertoire of acoustic, pheromone, and visual displays, and from females that make few precopulatory mate choices to those that have information about potential mates broadcast to them via several different channels. There are instances of licking, transfer of regurgitants, bright coloration, feathered legs, and reflective setae. Beneath the often splendid surfaces are a variety of phallic structures, vaginas, and sperm storage organs, which might respectively represent organs of communication and the mechanisms of copulatory or postcopulatory mate choice. This wealth of diversity superimposed upon a common theme makes fruit flies ideal subjects for studies, particularly comparative studies, that attempt to illuminate the evolution of mate choice and sexual competition.

We are certainly not the first to appreciate the potential of the Tephritidae and a number of influential papers of general importance have centered on fruit fly sexual behavior (e.g., Prokopy 1981; Burk 1982). What we attempt here is to place into context the enormous amount of sexual information that the chapters of this volume contain, and in doing so we have made an effort to point out unsolved problems as well as currently attractive hypotheses for the explanation of reproductive behaviors.

The authorship of this chapter is somewhat unusual; it is a true communal effort and JS should be seen as an editor rather than the principal author. To make the authorship of a particular section clear to the reader, authors' names are placed after the titles in the Table of Contents. A consequence of this style of multiple authorship is an occasional difference of opinion among the various contributors. We trust that the reader will not be disturbed by the heterogeneity of perspective and interpretation, but rather see these disagreements as indicating unsettled areas in the understanding of tephritid biology and opportunities for further study. A second, perhaps inevitable, consequence is a certain amount of redundancy; one author may readdress a situation that has been previously discussed by another in order to better make a point. Again, we hope that the reader will be patient with this format and see this "chapter" for what it is — a series of short discussions on the evolution of sexual behaviors among Tephritidae.

The chapter is organized into four sections, an introduction, a description of various sexual behaviors, a phylogenetically organized table that lists the presence or absence of particular behaviors, and discussions of the interactions between phylogeny and sexual behavior. The descriptions of sexual behaviors begin with those that bring the sexes together in time and space, followed by male agonistic interactions. Courtship signals, visual, acoustic, and pheromonal, are considered next and, after these, discussions of the content of courtship signals, the role predation may have played in the evolution of signals, and what factors might have influenced copulation durations. The phylogenetic table will provide readers with an idea of the scope and distribution of sexual behaviors, and should be an invaluable starting point to those interested in comparative studies.

Finally, two perspectives on the relationship of phylogeny and sexual behavior are considered: First, how sexual selection can result in divergence within populations and result in speciation and, second, how sexual behaviors can serve as characters in phylogenetic reconstructions.

## 28.2 A CATALOG OF SEXUAL AND AGONISTIC BEHAVIORS

### 28.2.1 MATING SITES AND RHYTHMS

#### 28.2.1.1 The Influence of Resource Distribution on Mating Sites

Resource distributions, particularly those of breeding sites, influence where and when the sexes meet (Emlen and Oring 1977). In tephritids, arguments have been made by Prokopy (1980) and Burk (1981) that different host fruit distributions lead to either male defense of oviposition sites or to male signaling with pheromones and acoustic displays (“calling”) away from oviposition sites. In brief, they proposed that when fruits are relatively rare (clumped), females can be predictably located at any particular oviposition site and that males that occupy such fruits can “force” females to mate. That is, it would be beneficial for females to mate with a resident male and then gain uninterrupted access to the resource rather than attempting to oviposit while being continually distracted by a courting male. Where there is little precopulatory female choice, there is little reason for males to invest in displays, and there is little if any courtship.

On the other hand, when resources are relatively abundant and homogeneous, females are not predictably located at any particular fruit, and males may either search among fruits or produce long-distance signals. Females have the freedom to leave fruits occupied by males and go to other, empty sites. This freedom of choice selects for males that advertise their qualities as mates and as a result courtship is complex. Males may aggregate either in good signaling sites, regions of female concentration, in the vicinity of unusually attractive males, or because of a female preference for grouped males (see Höglund and Alatalo 1995). The results are leks formed away from oviposition sites.

Both Prokopy and Burk argued that temperate species with narrow host ranges would be typified by fruit-guarding males with little courtship, but that polyphagous tropical species would form leks with complex displays. This is because highly polyphagous females presumably have so many choices of host that males can neither predict nor control access to oviposition sites.

Observations made over the intervening years have complicated the situation, and generalizations about temperate/tropic and monophagous/polyphagous distinctions are more difficult to make. For one thing, more examples have come to light of temperate and tropical monophagous species that form leks (e.g., Headrick and Goeden 1994). A peculiar tephritoid example of mating system diversity on a common substrate is found in two related species of piophilids that lay their eggs on moose carcasses (see Sivinski, Chapter 2). Males of one species form mating aggregations on the antlers, while the other males of the other species are dispersed over the body and perform mate-guarding behaviors (Bonduriansky 1995). Even within a species some males may guard fruit while others participate in leks (e.g., *Ceratitis capitata* (Wiedemann), Warburg and Yuval 1995; *Anastrepha suspensa* (Loew), Burk 1983).

However, the core principle of the Emlen and Oring/Prokopy-Burk model, that the abundance of hosts relative to the number of female fruit flies influences male distributions, remains an attractive vehicle for the exploration of tephritid mating systems. For example, in the genus *Anastrepha*, males of one species guard fruits, other species call (see Section 28.2.3 on sexual signals) from host plant leaves, and many of these leaf-calling species form male mating aggregations. Although important information on host and *Anastrepha* densities are often unavailable at present, testable predictions of the “relative abundance model” can be put forward. For instance, the fruit guarding *A. bistrigata* Bezzi would be expected to be abundant relative to its guava (*Psidium* spp.) host fruits. Although *A. bistrigata* is thought to be stenophagous (Norrbon and Kim 1988),

it is the relative scarcity of hosts and not monophagy or polyphagy per se, that is the critical factor in determining whether males find it profitable to wait for potential mates on a particular fruit, and that makes it unprofitable for females to search for unguarded oviposition sites.

In other apparently monophagous species, such as *A. hamata* (Loew), males call from host plant leaves rather than from fruits (M. Aluja, personal observation). The density model suggests that the fruits on these trees should typically be so abundant relative to females that a fruit-guarding male can no longer expect females to arrive at any particular fruit at a "profitable" rate. Furthermore, those females that alight on a male's fruit may be confident that there are unguarded and more easily exploited oviposition sites nearby.

While such males may now need to invest in more expensive advertisements, chemical and otherwise, to attract discriminating females, it is not clear why they abandoned fruit as a signaling platform. What advantages could leaves offer over fruit in these circumstances? It is possible that predators concentrate their foraging over fruits making residency dangerous (Hendrichs and Hendrichs 1990; see Landolt, Section 28.2.3.3). On the other hand, it may be that there are locations on host trees where fruits are not abundant, but which have high female densities because of favorable microhabitat. In *A. suspensa*, sexually inactive females and nonsignaling males accumulate in particular parts of host trees (Sivinski 1991). These same locations tend to be the sites occupied by sexually active males.

A particularly striking phenomenon among many species of leaf-calling males is their congregation into leks. These may occur in either polyphagous (e.g., *A. obliqua* (Macquart) and *A. suspensa*, Aluja and Birke 1993; Burk and Webb 1980) or monophagous species (e.g., *A. bezzii* Lima, M. Aluja, personal observation). Typically, several to many males signal with pheromones, acoustic signals, and perhaps visual displays from adjacent, or nearly adjacent, leaf territories which they defend from rival males (see Eberhard, Chapter 18, for discussion of lek definitions).

The significance of male fruit fly mating aggregations is not entirely understood. There are many hypotheses proposed for the evolution of insect leks (e.g., Shelly and Whittier 1997). Some of the more relevant ones are as follows.

1. Group calling amplifies the male signal and results in an average increase in the numbers of females encountered by the participants. However, the ranges of combined signals in most channels are at best additive, so there is no advantage to group signaling in terms of increased area covered. Pheromones are a possible exception to this rule (Bradbury 1981).
2. Females may prefer to choose mates from within groups of males, presumably because this facilitates accurate comparisons of potential mates or because mating inside a group protects females from predators.
3. Leks are an epiphenomenon. That is, they are simple accumulations of calling males in favorable microhabitats that might serve as resting sites for females, or in locations that are particularly suited to signaling, or in the neighborhoods of particularly attractive males.

Certain sites seem to be consistently used for lekking, suggesting that location plays an influential role in the formation of leks. As noted, *A. suspensa* leks form in the same areas that hold resting females, and these resting females often occur in clusters that have a structure that is superficially similar to that of a lek (Sivinski 1991). Such pockets of potentially high female concentration presumably constitute suitable sites for male calling. Lekking sites in *C. capitata* are stable over time. In a 60-day study by Shelly and Whittier (1995) only a few of the available trees consistently contained leks. There are a number of environmental factors, such as temperature, humidity, light, proximity to food sources, etc., that potentially influence the locations of leks (see Eberhard, Chapter 18). Males may also prefer to hold territories on sites where other males, or they themselves, had called previously. Pheromones are often deposited by males on leaf territory

surfaces (see Section 28.2.3.1 on acoustic signals), and some of the components remain there until at least the following day. Female *A. suspensa* respond to these deposited chemicals, and perhaps leaf territories (and lek sites) acquire value with repeated use (Sivinski et al. 1994).

With a further decline in the numbers of females relative to oviposition sites, a point is reached where it is no longer profitable for males to forage for mates on host plants. In such cases they may turn to alternative sites for calling and lek formation. Such "encounter sites" may originally have been navigation markers that concentrated females as they moved through an area (Parker 1978; e.g., swarm markers or hilltops, Sivinski and Petersson 1997), or else a location that is particularly suited for signal broadcasting. There appear to be no examples of this sort of mating system in *Anastrepha*, although the peculiar leaf-based calling behavior of *A. robusta* Greene (Aluja 1994) may prove to be so when its larval host plant is finally discovered. Occasionally, leks form in trees neighboring host trees (e.g., in *A. obliqua*, Aluja and Birke 1993 and *A. fraterculus* (Wiedemann), Malavasi et al. 1983), but from the flies' perspective these are probably sensed as particularly favorable extensions of a host plant. However, there are tephritids in other genera that form leks on nonhost plants, for example, an undescribed *Blepharoneura* species from Costa Rica (Condon and Norrbom, Chapter 7) and *Procecidochares* sp. nr. *minuta* from the American southwest (Dodson 1987).

### 28.2.1.2 Species Isolation and the Timing of Sexual Activity

#### 28.2.1.2.1 *Anastrepha*

Flies in the genus *Anastrepha* offer a unique opportunity to analyze the evolution of calling and mating rhythms. As reviewed by Aluja et al. (Chapter 15), there is an extremely wide range of calling rhythms in this genus, from species that call in the early morning hours (sunrise) to those that do so during the late afternoon (sunset). The most parsimonious interpretation of the evolution of such varied patterns is the gradual selection for sexual activity rhythms that limit interspecific interactions and hybridization. If so, the timing of sexual activities in sympatric species should diverge.

The Caribbean fruit fly (*A. suspensa*) and the West Indian fruit fly (*A. obliqua*) purportedly share a center of origin, and have daily patterns of calling that are almost perfectly reversed (Aluja et al., Chapter 15). While *A. obliqua* calls preferentially in the morning, *A. suspensa* calls during the afternoon hours. The calling patterns of three species living in sympatry in Mexico, *A. fraterculus*, *A. striata* Schiner, and *A. ludens* (Loew), also differ sharply among themselves (Aluja et al., Chapter 15).

An interesting phenomenon with respect to calling and mating rhythms is the appearance of differences in patterns among geographically distinct populations of the same species. For example, males of *A. serpentina* (Wiedemann) from the Pacific state of Chiapas in southwestern Mexico exhibit a bimodal pattern with peaks between 08:00 and 10:00 and 14:00 and 17:00 hours while those from the Gulf state of Veracruz only call from 11:00 to 17:00 hours (Aluja et al., Chapter 15). A similar geographic variation in calling rhythms is observed in *C. capitata*.

#### 28.2.1.2.2 *Toxotrypana*

Information on this genus is restricted to one species, *T. curvicauda* Gerstaecker. Interestingly, reports vary sharply with respect to geographical origin. Individuals in populations from Florida call in the late afternoon hours (Aluja et al., Chapter 15). In sharp contrast to this, populations from the state of Morelos, Mexico call from late morning to early afternoon hours (depending on the time of year). It is possible that these differences reflect the presence of two biotypes or even two different species.

#### 28.2.1.2.3 *Bactrocera*

Flies in the genus *Bactrocera* (formerly *Dacus*) are a diverse group. Species such as *B. aglaiae* (Hardy), *aquilonis* (May), *cacuminata* (Hering), *cucumis* (French), *cucurbitae* (Coquillett), *diversa* (Coquillett), *decurtans* (May), *dorsalis* (Hendel), *endriandrae* (Perkins and May), *halfordiae* (Tryon), *jarvisi* (Tryon), *kraussi* (Hardy), *musae* (Tryon), *opiliae* (Drew and Hardy), *passiflorae*

(Froggatt), *scutellaris* Bezzi, *tau* (Walker) (= *hageni* Meijere), *tryoni* (Froggatt), and *zonata* (Saunders) call and mate at dusk under low light intensity (see reviews by Fletcher 1987 and Smith 1989 for specific references). In contrast, there are some species, such as *B. expandens* (Walker), *oleae* (Rossi), and *neohumeralis* (Hardy), that mate during the middle of the photophase under high light intensities (Haniotakis 1974; Fletcher 1987). Finally, species such as *B. tenuifascia* (May) and *tsuneonis* (Miyake) initiate copulation during any time of the day. Why are there these differences? As previously suggested for species of *Anastrepha*, time of mating may be an effective barrier to hybridization between species. This can be illustrated in the case of the closely related species *B. tryoni* and *B. neohumeralis*. The former mates only at dusk, while the latter does so at midday. Perhaps the large number of species that mate at dusk do so in species-specific locations in their native forests.

#### 28.2.1.2.4 *Ceratitis*

The mating rhythms of only two species of this genus have been studied, the sympatric *C. capitata* and *C. rosa* Karsch. Caged, wild *C. rosa* on Reunion Island mate only in the late afternoon (peak between 18:30 and 19:00 hours), while sympatric *C. capitata* do so preferentially in early morning hours (peak between 07:00 and 09:00 hours with a smaller peak between 13:00 and 14 hours; a few individual *C. capitata* mate throughout the day; Quilici and Franck 1997).

*Ceratitis capitata* has become widespread around the world, and there appears to be a geographic pattern in *C. capitata* mating activity. In Guatemala, peak calling activity was reported between 11:00 and 14:00 hours. In Hawaii there were two peaks, a small one at 10:00 and a bigger one between midday and 14:00 hours (Whittier et al. 1992). Note that this is the reverse of the calling pattern on Reunion Island. In Egypt, the bimodal pattern resembles that reported for Reunion Island, a main peak in the morning (before the hottest part of the day) and a smaller one in the afternoon. Finally, in Chios (Greece) and Israel peak mating activity occurred during midday. In locations where interactions with close relatives are not possible (Greece, Israel, Guatemala, and Hawaii), mating activity occurs at times similar to the period of activity in *C. rosa* (i.e., afternoon hours). Thus, afternoon calling by *C. capitata* in regions of allopatry may represent a temporal shift into a block of time filled by the calling of *C. rosa* in areas of sympatry. If so, this further supports the hypothesis that varying mating rhythms evolved as a mechanism to restrict hybridization.

#### 28.2.1.2.5 *Rhagoletis*

Patterns of mating in *Rhagoletis* also differ according to species. This could be interpreted in a manner similar to the above (see Propkopy and Papaj, Chapter 10).

### 28.2.2 AGONISTIC BEHAVIOR

Defining agonistic interactions as “aggressive or defensive social interactions between conspecific individuals” does surprisingly little to elucidate what does or does not qualify as agonistic. A wide range of behaviors have been considered agonistic, and it is difficult to delineate the category clearly. While an extreme activity such as hostile, physical combat is readily viewed as aggressive, less pugilistic behaviors such as wing displays and other body postures are more difficult to classify. Noncontact interactions have often been described as agonistic in studies of tephritids and the justification seems to come mainly from assessment of the context of the encounter. For example, a particular wing movement by a male may be interpreted as a courtship signal when directed toward a female, but an agonistic display when directed intrasexually.

Most of us think of agonistic interactions as those that involve *fighting*. Indeed, Scott and Fredricson (1951) coined the term *agonistic* with specific reference to actions related to fighting. In the lay vernacular, fighting need not involve physical contact. Simply the threat of an action that would negatively impact the well-being (fitness) of another individual is often considered a fight (e.g., angry shouting by humans). Unfortunately, until neurological assessment of the motivation

behind all nonhuman animal behaviors is possible, we will be forced to continue our speculation regarding the function of many potentially agonistic actions. Herein, we will focus on the more blatant examples of fighting in tephritids, but continue to consider ambiguous behaviors such as wing displays as likely components of agonistic activity. First, we review the theoretical framework that allows us to predict who should fight and when; and then we ask whether tephritids appear to follow predictions from this theory.

Ever since Darwin (1871) formalized the observation that males are more prone than females to exhibit overt intrasexual contests, there have been refinements of the theory attempting to explain why this is so. In a nutshell, females are expected to be the more discriminating sex in mate choice due to their overall lower variance in mating success and greater parental investment in offspring (Bateman 1948; Trivers 1972). Selection should therefore favor males that devote more of their total reproductive effort toward mating effort. Competition among conspecific males to attract, encounter, or monopolize potential mating partners leads to many contest situations.

This is not meant to suggest that females should never act aggressively. There is little doubt that females in most animal species routinely or occasionally direct aggression toward males when they are not receptive to mating attempts. Aggressive nonreceptivity can include charging, biting, striking, and other offensive behaviors. Since the message conveyed is likely to be unambiguous and males usually have little to gain by "fighting back," agonistic interactions of this type are not expected to be prolonged or highly ritualized. Even in the many described instances of "forced copulations" among tephritid species, the actions of males are most appropriately viewed as "coercive" rather than fighting. Female aggression toward males in tephritids is often observed by researchers (see taxon-specific chapters in this volume), but there are no reports of prolonged or escalated contests.

Aggressive, intrasexual competition is expected among females if a required resource (e.g., oviposition substrate or adult food source) is limited relative to the number of individuals attempting to use it. Tephritid females have been observed physically aggressing conspecific and heterospecific intruders while at food or oviposition sites (e.g., Pritchard 1969; Biggs 1972; Dodson 1982; and unpublished data; Papaj et al. 1989; Headrick and Goeden 1994). However, severe resource limitations are rare (see Dodson, Chapter 8, for the only documented case); therefore, prolonged combat is not expected from a cost/benefit perspective. If monopolizing a site requires a high energy expenditure or excessive time commitment, then seeking other sites may be the best option as long as they are accessible. Selection should favor less costly alternatives when competition for resources is not extreme. The well-documented examples of oviposition-detering pheromones within tephritids (Propkopy and Papaj, Chapter 10) suggest that all parties gain from signals that verify the earlier presence of a competitor.

Male-male aggressiveness, on the other hand, is expected to be common. Male reproductive fitness is limited primarily by the number of matings acquired (Bateman 1948). Receptive females are therefore a limiting resource for males (except in the rare instances of a female-biased operational sex ratio, Emlen and Oring 1977). Animals such as male tephritids effectively compete for mates every day of their adult lives, excluding instances of reproductive diapause. It is thus not surprising that males routinely display agonistic behaviors whenever they encounter one another, even when no females or resources are currently present. However, the most intense combat is expected when females or female-required resources are distributed in such a way that individual males can guard them and monopolize access (Brown and Orians 1970), leading to female or resource defense mating systems (Emlen and Oring 1977). Habitual aggression is also expected when males are competing for space at display sites to which females come only for mating (lek or landmark mating systems). The least aggression should occur within species that exhibit a distribution of females and resources that are not clumped and cannot be monopolized, and in which males compete in isolation to find females rather than advertising and waiting for females at leks ("scramble competition" *sensu* Thornhill and Alcock 1983).



Examples of the scramble competition mating system and the predicted low-intensity agonistic interactions are represented by the gall-forming species included in Headrick and Goeden's (1994) circumnatal mating system category. Males of these species typically *stalk* (Headrick and Goeden 1994) females in isolation and only occasionally confront each other. Even when male–male encounters occur, there is little incentive for lengthy fighting since any females in the vicinity are likely to be moving on. Dodson (1987a, b) provided a detailed account of the mating and agonistic behaviors of a representative species (*Aciurina trixa* Curran).

Lek mating systems have been well documented within the family (Sivinski, Section 28.2.1.1) and virtually all accounts include descriptions of frequent male–male agonistic interactions. With some interesting exceptions, lekking flies are mainly polyphagous species (Sivinski and Burk 1989). Since a high proportion of the mating in these species occurs at the lek (most, if not all exhibit mating at oviposition sites as well), there is strong selection on males to acquire a position within the lek and perhaps even to compete intensely for the “best” positions therein (Sivinski and Burk 1989). These species represent a good test of the theoretical expectations of relative fighting intensity. In species where the highest proportion of mating success is achieved at leks (many species of *Anastrepha*, *Ceratitis capitata*?), fighting intensity should be greater at these display sites than at secondary mating sites. By contrast, when a resource-based mating strategy produces more matings within a species than the leklike alternative (some *Rhagoletis*?), fighting should be less intense at the leks.

It is a logical assumption that female-required resources will be scarce more often for monophagous than for polyphagous species. Indeed, of the reported cases of resource defense mating systems in tephritids, all involve species that are monophagous or oligophagous, and the resource being defended is typically an oviposition substrate — for example, in *Anastrepha bistrigata* (Morgante et al. 1993), *Dacus longistylus* (Wiedemann) (Hendrichs and Reyes 1987), *Phytalmia* spp. (Dodson 1997), *Rhagoletis boycei* Cresson (Papaj 1994), *R. completa* Cresson (Boyce 1934), *R. juglandis* Cresson (Papaj 1994), *Toxotrypana curvicauda* (Landolt and Hendrichs 1983). Other cases of resource defense involve nutritional resources for females that are either naturally occurring or male produced, for example, plant wounds guarded by *Paracantha gentilis* Hering (Headrick and Goeden 1990) or spittle masses guarded by *Euaestoides acutangulus* (Thomson) (Headrick and Goeden 1996), salivary secretions produced and guarded by male *Eutreta novaeboracensis* (Fitch) (Stoltzfus and Foote 1965) and *Neaspilota viridescens* Quisenberry (Goeden and Headrick 1992, and unpublished data). Males of several species are known to produce salivary secretions in the form of mounds on which females feed (Freidberg, Section 28.2.3.4). Although that involving *E. novaeboracensis* is the only published account of agonistic behavior expressly associated with guarding a mound, further observations are likely to reveal such behavior for some if not all of these species.

Having considered the ecological characteristics that predispose certain species to agonistic behavior, it is interesting to ask what kind of fighting is expected to occur. To this end, game theory models have greatly clarified our understanding of the nature of contest structure (Parker 1974; Maynard Smith 1982; Reichert 1998). The emergent consensus is that animal contests are designed to gain the maximum information about the quality, ability, and motivation of an opponent with as little cost as possible. All participants potentially benefit from the acquisition of information that reliably forecasts the outcome of a contest without expenditure of additional energy or the liability of greater risk resulting from further escalation. Actual fighting should be limited to instances in which opponents are so evenly matched (through combinations of fighting prowess, current condition, motivation, etc.) that the outcome is uncertain based on the information available early in a contest. In other words, escalation of contests is expected only when it is difficult for the participants to determine the superior opponent without extended assessment or when the value of the contested resource is especially high (Sigurjónsdóttir and Parker 1981).

Tephritids have little in the way of physical attributes that would lead us to expect injury risks in their agonistic encounters, and we are not aware of any report of damage inflicted on one male by another. Thus, their conflicts are best represented by the war of attrition models in which contest



costs arise in the form of time and energy expenditures and winners are those that opt to persist longer (Maynard Smith 1974; Parker and Thompson 1980). Contests such as the stiling behavior described below may represent the most extreme method used by evenly matched tephritid combatants to test the persistence quotient of each opponent.

The extensively documented wing displays (Headrick and Goeden 1994) employed by males in almost all aggressive encounters may provide the most basic information about the size, vigor, and/or motivation of a contestant. Acoustic and pheromonal signals could play similar roles or possibly represent a second level of information if they are more costly to exhibit. Should these types of information fail to clarify the probable outcome of a contest sufficiently (i.e., neither contestant retreats), physical contact appears to be the final assessment mode. A perusal of the behavior chapters in this volume reveals that tephritid males make both gentle and forceful contact with each other wing-to-wing, wing-to-body, head-to-head, mouthpart-to-mouthpart, legs-to-legs, legs-to-wings, legs-to-body, and legs-to-head. We assume that all of these actions involve a tactile signal, and that at least some may also provide chemical cues. Contact with the legs has been described variously as boxing, sparring, pawing, striking, batting, grappling (and even "belaboring each other with their forelegs" [Brooks 1921]). They butt heads and push against each other with mouthparts, heads, and legs. These actions often appear frenetic, but can be very complex and seemingly choreographed in some species (e.g., Headrick and Goeden 1990; Headrick et al. 1995; Goeden et al. 1998).

Males mounting other males in a copulatory manner is a fairly common behavior observed by tephritid researchers and has been interpreted by most authors as evidence of poor gender discrimination by males. Such behavior could be a form of aggression rather than a "mistake" and closer examination of the activities leading up to this behavior has suggested this interpretation in one case. Iwahashi and Majima (1986) discovered distinctive behaviors preceding such mountings, indicating that males recognize the sex of the intruders prior to making contact with them. While it is reasonable to expect mistakes by these animals, this finding should serve as a reminder that extremely careful examination is required to detect such subtle details of motivation.

The most-escalated fights described thus far for tephritids have a similar composition. Males that have confronted each other head-to-head rise up on their middle and hind legs. Their unconstrained forelegs (and sometimes the middle legs, Boyce 1934) are then used to box at each other or are raised above their heads and held aloft, waved, or batted against the legs of their opponent. This form of fighting is illustrated in Figure 21 of Headrick and Goeden (1994) and is characteristic of *Euarestoides acutangulus*, *Euaresta stigmatica* Coquillett, *Tephritis stigmatica* (Coquillett), *Trupanea jonesi* Curran (Headrick and Goeden 1994), *Phytalmia* spp. (Dodson 1997), and the *suavis* group of *Rhagoletis* (Brooks 1921; Boyce 1934; Papaj, unpublished data). In most of these species, the mouthparts of the males are in contact during some or all of the time they are stilted. A variation is found in some *Phytalmia* species in which the epistomal margin of the face is used as a pushing surface in these upright contests (Dodson 1997). The intensive male-male fighting exhibited by the papaya specialist *T. curvicauda* does not include stiling, but the head and thorax are often elevated during contests at fruit territories (Landolt and Hendrichs 1983). Fighting similar to that of *T. curvicauda* was described in laboratory observations of *R. pomonella* (Walsh) (Biggs 1972).

Reinforcing the point made earlier, all of the species exhibiting this escalated fighting style are monophagous or stenophagous species and thus are known or presumed to be defending a limited resource with the prospect of increased mating encounters. The exceptional species is *T. jonesi*, which has the broadest known host range (104 species in eight tribes of Asteraceae) of any North American tephritid (Goeden et al. 1998). The intensive male-male fighting was observed in two instances in the laboratory (Goeden et al. 1998), and the location of this fighting in the field awaits observation. Perhaps this species defends a limited resource separate from an oviposition substrate, as does *E. acutangulus*; or consists of host races isolated on subsets of the known hosts. If *T. jonesi* is determined to be a polyphagous species fighting so intensely at a nonlimited resource, we will need to rethink our theory.

In sum, the theoretical models of animal conflict and agonistic behavior in tephritids seem to be in concert. Fighting is more frequent in males than females. Fighting is least intense in species exhibiting scramble competition (i.e., circumnata) mating systems, more pronounced at leks, and escalated where required resources are economically defensible. A hierarchy of behaviors appears to be utilized, consistent with the expectation that contests will be settled as soon as sufficient information is obtained that reliably predicts the winner. Finally, the most energetically and temporally costly behaviors are used only when necessary in these fascinating tephritid wars of attrition.

### 28.2.3 COURTSHIP

#### 28.2.3.1 Acoustic Signals

Male, and occasionally female, fruit flies sometimes make rapid wing motions in sexual contexts (Tephritinae — e.g., Greene et al. 1987; Trypetinae — e.g., Burk and Webb 1983; Dacini — e.g., Kanmiya 1988). These movements could typically be characterized as hamation, evanation, or synchronic supination in the terminology of Headrick and Goeden (1994), and are often correlated to pheromone release and related behaviors, such as abdominal pleural distention and/or dabbing the substrate with the proctiger (e.g., Headrick and Goeden 1994; see Glossary, Chapter 33).

It has been supposed that the function of the movements is to waft pheromones into the airstream or toward an approaching female (e.g., Sivinski et al. 1994). In the genus *Anastrepha* all species evert the proctiger to expose pheromone-dampened anal membranes; however, primitive species such as *A. cordata* Aldrich and *A. aphelocentema* Stone do not simultaneously fan their wings while chemically signaling in the absence of females (Aluja et al., Chapter 15; see similar behavior in the sister genus *Toxotrypana*, Sivinski and Webb 1985b). More derived *Anastrepha* species wing-fan as they occupy leaf territories in leks (e.g., Burk 1983; Aluja and Birke 1993). Calling by male *A. cordata* and *A. aphelocentema* has not been observed in nature; perhaps they will be found to call, like *T. curvicauda*, on or near fruit whose additional female-attracting odors may allow them conserve the energy that would otherwise be spent in wing fanning. Alternatively, it may be that competition from nearby males in mating aggregations results in males expending considerable energy to establish their precise location. That is, females arriving at lek sites might find it easier to discriminate males with strong individual pheromone plumes generated by wing fanning.

While pheromone dispersal may have been the original purpose of wing fanning, the sounds produced by such movements, in at least some instances, have taken on a signaling significance of their own (e.g., Aluja et al., Chapter 15). Even additional sound-producing structures, such as the “pecten” (abdominal setae that are struck by the wing) of *Bactrocera cucurbitae* (Coquillett) (Kanmiya 1988), have evolved. In *A. suspensa* and *C. capitata* removal of the wing does not entirely mute the sound, suggesting that thoracic vibrations in addition to wing movement may be involved in sound production (Keiser et al. 1973; Sivinski and Webb 1985a).

There are several additional behaviors and structures that imply an acoustic communications role for wing movements. Female *C. capitata* perform high-speed wing movements identical to those of males (Sivinski and Webb 1989). The reason for these movements is obscure, although they may incite male courtship by mimicking a rival (Arita and Kaneshiro 1983). Since there is no evidence that females produce a pheromone (Heath et al. 1994), mimetic females are probably producing signals that have some acoustic (or visual) significance. This suggests that the original male wing motions, on which the female signals are modeled, are also likely to be acoustic displays rather than mere by-products of chemical dispersal behaviors. In another instance, *R. juglandis* males control access to individual walnuts and are not known to produce pheromones. However, they wing-fan as they approach females that have come onto their fruit and the low-frequency sound produced may serve as a courtship song (see Prokopy and Papaj, Chapter 10; alternatively, they may be directing host volatiles at females).

In the relatively well-studied case of *A. suspensa*, there are at least two forms of acoustic signals ("calling" in the vocabulary of Headrick and Goeden 1994). One takes place when the male expands its pleural glands and dabs pheromone unto the leaf territory surface ("calling song"), and the other, when the male mounts the female and attempts to engage her genitalia ("precopulatory song"; Sivinski et al. 1984). Calling songs elicit responses from virgin females and males, but not from mated females, and their rate of production and structure change with circumstance. For example, pulse trains (episodes of wing beating) increase in duration in the presence of males, and the interval between pulse trains decreases when females are nearby (Sivinski and Webb 1986). The precopulatory song is very energetic and its sound intensity was shown experimentally to be an important factor in determining whether females would allow singing males to copulate (Sivinski et al. 1984). As mentioned earlier, there is a third form of acoustic sexual signal, made only as males orient toward and court a nearby female. A relatively well-documented instance occurs in *T. curvicauda*, a member of the sister genus of *Anastrepha* (Sivinski and Webb 1985).

### 28.2.3.2 Visual Signals

#### 28.2.3.2.1 Color and Pattern

As brief examinations of Foote et al. (1993), White and Elson-Harris (1992), and other taxonomic works will testify, many tephritid bodies and wings are marked with bands, spots, and blotches. In addition, the eyes are often brightly colored and sometimes banded or otherwise patterned (e.g., *Anastrepha*, *Ceratitis*, or *Phytalmia* spp.; Color Figure 20\*; and see Moffett 1997). There is an understandable assumption that these colors, particularly when sexually dimorphic, serve communicative functions (e.g., Burk 1981). One plausible example are the violet pink and green-striped eyes of *Phytalmia megalotis* Gerstaecker that flank a pink face, which is itself extended laterally to form pink- and black-trimmed antlers (Wallace 1869). Such antlers have been shown to advertise size in agonistic communications among rival males (Dodson, Chapter 8), and it is likely that the facial colors and those of the eyes contribute to the display. Likewise, the sexually dimorphic eye colors and contrastingly colored capitate anterior orbital setae of *C. capitata* probably produce male visual signals (Eberhard, Chapter 18). Another display that seems almost certain to be a visual signal, and one that uses colors on a different part of the body, occurs in the tephritine *Eutreta diana* (Osten Sacken). In this species, the midfemora are black with yellow tips (Headrick and Goeden, Chapter 25), and are lifted (abducted) by the male during courtship. At the same time it holds its wings arched over its back, providing a dark background for the femoral display.

While there is a good deal of anecdotal natural history, there is little experimental evidence addressing intraspecific fruit fly visual communication. Female *C. capitata* will turn toward males separated from them by a pane of glass when the latter vibrate their wings (Féron 1962), and males of the same species are more likely to begin pheromone calling when kept in vials with mirrors (McDonald 1987). Females are more likely to oviposit when they perceive wing-waving by a female already present on a fruit (Prokopy and Duan 1998). However, the best documented cases for visual signaling are interspecific in nature and concern the "misleading" information transmitted by wing patterns of species such as *Zonostemata vittigera* (Coquillett) and *R. zephyria* Snow to jumping spiders (Greene et al. 1987; Mather and Roitberg 1987). When seen from behind, some pigmented bands create the illusion of a salticid seen face-on and the resemblance deters attacks.

Support for visual communication through color patterns on wings might be obtained by considering the behaviors, and the absence of certain behaviors, in taxa which lack wing patterns. The only tephritoid family with typically unpatterned wings is the Lonchaeidae, and this is the only family in which aerial swarm-mating systems are common (Sivinski, Chapter 2). It may be that patterns are imperceptible in flying individuals and useless for communicating within swarms. Note also that fruit flies without distinctively patterned wings such as *T. curvicauda* and *Bactrocera* spp. do not have many of the stylized wing movements typical of other tephritids (Sivinski and Webb 1985b; Landolt, Chapter 14).

\* Color Figures follow p. 204.

However, if wing patterns function in sexual communication, it seems surprising that sexual dimorphism appears to be rare, although there are instances of considerable differences; for example, in *Aciurina idahoensis* Steyskal, female wings are striped and males' spotted (Headrick and Goeden, Chapter 25), while in the related *A. semilucida* (Bates) females again have striped wings while those of the male are fully infuscated. In addition to being uncommon, those sexual dimorphisms that do occur are often not what is expected, with male wings being fainter than females' and/or bearing interrupted or missing markings (e.g., many *Trupanea* spp.; Foote et al. 1993). There has apparently been no thorough search for ultraviolet markings on the wings of fruit flies, and until such a survey has been completed it may be premature to discount the possibility of widespread sexual dimorphism.

#### 28.2.3.2.2 Ornaments

Occasionally, male tephritids bear elaborate or novel structures that presumably have been sexually selected to function as signaling devices (e.g., Sivinski 1997). The above-mentioned antlers of *Phytalmia* species are an example. In this instance, the ornaments communicate male size to rivals during agonistic interactions for the control of oviposition sites (Dodson, Chapter 8). There is a variety of ornaments whose functions may vary as well. A few examples give a flavor of the range.

**Head:** While the rain forests of New Guinea and vicinity contain the antlered *Phytalmia*, even seemingly mundane locations such as the British Isles harbor several fruit flies with marvelously modified heads (White 1988). An impressive row of enlarged bristles projects from the lower face of the trypetine *Chetostoma curvinerve* Rondani. Forward-jutting projections on the frons of another trypetine, *Stemonocora cornuta* (Scopoli) also bear long, stout setae — in the United States similar setae arise from the upper portion of the head of the trypetine *Paramyiolia rhino* (Steyskal) (Foote et al. 1993). In the terelliine, *Cerajocera ceratocera* Hendel, it is the pedicel (second antennal segment) that sticks out like a bristled horn. See Han (Chapter 11) for additional examples of tephritids with projections or modified setae on the head.

Other examples of specialized head setae occur in *Ceratitis* subgenus *Ceratitis*; the reflective, paddlelike hairs are especially well developed in species such as *C. catoirii* Guérin-Ménéville (White and Elson-Harris 1992) and *C. caetrata* Munro (Munro 1949; see Eberhard, Chapter 18).

**Thorax:** The front basitarsi of *Euphranta maculifemur* (Meijere) is broadened and concave (Hardy 1973). In several species of *Ceratitis* the midlegs are "feathered" with long setae on the tibia or tibia and femur (e.g., Freidberg 1991; White and Elson-Harris 1992; De Meyer, Chapter 16).

**Abdomen:** Male *Trupanea brunneipennis* Hardy have a mass of strong yellowish bristles along the fifth tergite of the abdomen (Hardy 1973). *Copiolepis quadrisquamosa* Enderlein from New Britain and New Guinea is dramatically attired with long bird-of-paradise-like "plumes" projecting from the abdomen (Enderlein 1920).

The functions of structures such as those listed above are often enigmatic, particularly when so few observations of courtship have been made, and they may or may not function in visual displays. For example, there is a large downward-pointing projection from the front femur of male *Ectopomyia baculigera* Hardy (Hardy 1973), but it is possible that such a structure is a mechanism used to secure mounted females — see projections on the legs of *Phytalmia* spp. (Dodson, Chapter 8), and the enlarged forefemora of *Aciurina* spp. (Headrick and Goeden, Chapter 25). Even if the ornaments are used in communication they may perform in a different, nonvisual, channel; for example, "feathered" legs might provide tactile stimuli.

#### 28.2.3.2.3 What Do Displays Mean?

Courtship activities and structures are often hypothesized to have evolved in one of several contexts (e.g., Sivinski 1997; Endler and Basolo 1998). One of these general theories supposes that some information of importance to the receiver is contained in the signal, although selection may favor exaggeration in the display. MacAlpine's (1979) hypothetical account of the evolution of stalk eyes in Platystomatidae (Tephritoidea) is a particularly elegant example of this process, albeit one that

describes the evolution of an agonistic rather than a courtship display (Sivinski, Chapter 2); tephritids such as *Pelmatops ichneumoneus* (Westwood) also have stalk eyes (Wilkinson and Dodson 1997; see also Dodson, Chapter 8). Suppose that flies entering a face-to-face agonistic interaction avoid costly combat by first estimating the size of their opponent and then decamping if the other fly is larger. If size is determined by the extent that the margins of the opponent's head (eyes) overlaps those of the observing fly, then an atypically broad head provides a psychological advantage. Of course, as broad heads become more common, then still greater head expansion is required to carry out a successful bluff against a typical opponent. This results in an "arms race" that pulls eyes farther and farther apart. The race concludes when the danger and expense of the ornament equals the competitive advantage it provides. Accordingly, while stalk eyes were originally deceitful, in the end they became honest advertisements since only the largest and most vigorous individuals could wield the largest ornaments (such ornaments may also give insight into the information-processing capacities of flies; it is difficult to imagine animals capable of synthesizing information from different perspectives, like cats or squirrels, evolving stalk eyes).

Honest signals, including stalk eyes, are of interest to mate-choosing females as well as rivals. In the diopsid *Cyrtodiopsis whitei* (Curran) females preferentially gather around males with long eye stalks (Burkhardt and Motte 1988).

Another perspective on "honest advertisements" supposes that during the evolution of ornaments and elaborate behaviors it is the expense of displaying that is selected from the very start (e.g., Zahavi and Zahavi 1997). Expensive and dangerous "handicaps" reflect the underlying qualities of the signaler. The fact that an animal has survived in spite of its display burden gives a potential mate greater insight into the signaler's abilities than what could be determined from the mere presence of an unornamented and untested rival.

Whether a signal has evolved through an "arms race" between emitters and receivers, or through competition among "reckless signalers" striving to guarantee their hardiness, there is the supposition that the messages, at least those directed at the opposite sex, contain evidence of genetic quality ("good genes"). What exactly might these advertised qualities be? There is an extensive literature on the "substance" of intersexual signals, one too large to address here. But, size and vigor (e.g., Burk and Webb 1981), low genetic loads (as expressed by high levels of bilateral symmetry; e.g., Thornhill 1992), and ability to resist pathogens and parasites (e.g., Hamilton and Zuk 1982) are all potentially heritable qualities that appear to interest females of certain species (see also Eberhard, Chapter 18). It is also possible for males to advertise a material rather than genetic quality (see Freidberg, Section 28.2.3.4).

At this time, there is little direct evidence for "good genes" content in male fruit fly displays directed toward females. Many structures and colors used in the displays of tephritids, as well as mammals and birds, are located on the head (e.g., capitate setae and bristled projections). The front of the head is likely to be the "signal platform" closest to the courted or threatened conspecific. Zahavi and Zahavi (1997) have argued that head extensions might clearly display the orientation of the head, and so serve as proof that the displaying animal is looking directly and uninterruptedly at the receiver. Since focused staring presumably makes the signaler vulnerable to predation, it may constitute a dangerous handicap and be an expression of "self-confidence"; that is, insects that behave in such a way, and are still alive, will tend to have superior senses and reflexes. If so, would female fruit fly orientations toward courting males be shorter in duration than male orientations to females, and do females "glance" about more often than males? Male *C. capitata* with more symmetrical anterior orbital bristles have greater mating success (Eberhard, Chapter 18). However, the orientation of the bristles during courtship may make them difficult to observe, and bristle symmetry might only reflect a general symmetry that is scrutinized by potential mates through other, more noticeable, structures. Expensive acoustic signals, such as the copulatory song of *A. suspensa*, have been hypothesized to be the result of discriminating females making increasing demands on males to display their vigor and energy reserves (Sivinski et al. 1984; Aluja et al.,

Chapter 15). Athleticism may be demonstrated by the males of some *Rhagoletis* spp. which initiate copulations either on leaf surfaces or in *midair* (e.g., Prokopy 1976).

A second explanation for the evolution of courtship signals supposes that there is no information embedded in male motions, structures, or colors that could independently corroborate a male's suitability as a sire. Rather, an arbitrary preference in females for the most extreme examples of a particular male trait can lead to "Fisherian runaway sexual selection"; that is, such a preference results in the presence of genes for both the extraordinary signal and a preference for the extraordinary signal in both males and females which can generate a sort of "chain reaction" self-selection for the increasingly extreme (see a lucid explanation in Dawkins 1986). There is debate over the likelihood of runaway selection in insects. Alexander et al. (1997) have argued that insects are typically ill-suited to this form of selection since it requires that females sample a range of males and then choose the extreme. They argue that most insects are too short lived to acquire broad experience of potential mates and lack the capacity to recall and compare the information they do obtain. This view, and the evidence supporting it, has been criticized by Eberhard (1997). Zahavi and Zahavi (1997) point out that extravagant signals are sometimes used both in sexual *and* agonistic encounters, and that runaway selection is unlikely to account for the evolution of an intrasexual signal. That is, males unburdened by ornamentation will presumably defeat those that are handicapped by an ostentatious display that had no correlation to size or vigor during the early stages of its evolution.

A third explanation, and one supported by a growing number of examples, is that signals evolve to exploit biases in their receivers. That is, a particular ornament or coloration evolved simply because females were predisposed to respond to the early stages of the signal. A particular bias might be a side effect of "other mate choice preferences, responses that evolved to locate prey or avoid predators, and limitations imposed by the more general operating principles of neural and cognitive systems" (Ryan 1998). For example, females of wolf spider species without ornamented males preferentially respond to the courtship displays of ornamented males of related species (McClintock and Uetz 1996). This sort of untapped female "preference" (or vulnerability to manipulation) has been found in amphibians, fish, and birds as well (Ryan 1998). Similar experiments might be attempted with the genus *Ceratitis*, some species of which have large capitate setae while others do not (see White and Elson-Harris 1992). Might tephritid wing motions and patterns, originally employed to distract or confound predators, have an effect on females as well and become secondarily useful in sexual communication (see Section 28.2.3.2.1)?

### 28.2.3.3 Predation and the Evolution of Sexual Behavior

#### 28.2.3.3.1 Introduction

The sexual behavior of tephritid fruit fly species is quite varied, with many types of signals and strategies, and both intrasexual and intersexual interactions. The sexual behavioral repertoire evolved within a given species of Tephritidae may be a result in part of ecological parameters, such as host breadth, latitude, and climate (Emlen and Oring 1977; Prokopy 1980), as well as phylogenetic history. In many species of Tephritidae, selection pressures exerted by predation may also have had impacts on the signaling and strategies involved in the seeking and selecting of mates.

Monteith (1972) found that apple maggot flies in apple trees were not predated and Prokopy (1977) considered nonteneral adult tephritids to be generally free of predation. However, others report predation on adult fruit flies by wasps, odonates, mantids, and spiders (Brittain and Good 1917; Greene et al. 1987; Mather and Roitberg 1987; Van der Valk 1987; Whitman et al. 1988; Hendrichs and Hendrichs 1990; Hendrichs et al. 1994). Fruit flies are probably eaten also by vertebrates such as frogs, lizards, and birds. Although most species of tephritids are agile fliers and able to evade predators, they are also generally defenseless, both physically and chemically.

Fruit flies may be particularly prone to predation when they are engaged in mating (Hendrichs and Hendrichs 1998) as well as other sexual behaviors such as courtship interactions. When engaged



in such activities, they are likely to be more conspicuous or apparent to predators, may be less mobile (when in copula), and they also are likely to suffer a decrease in attentiveness. If an insect is displaying or signaling, it may place itself in a relatively open location, either to signal from a resource at that site or to increase its apparency to conspecifics. It would then also be more conspicuous to predators at such signaling sites. When signaling, whether visually, acoustically, or pheromonally, a fruit fly may also inadvertently advertise its presence to predators by those same signals. Additionally, it seems likely that male and female flies interacting in courtship, or males involved in territorial and related agonistic interactions, would be less apt to perceive danger from approaching predators, and might be more susceptible to predation. It is easy to imagine that predation pressures may have influence, via natural selection, on the sexual signaling and location of sexual interactions of tephritid fruit flies, and that specific morphological, physiological, and behavioral traits might be adaptive responses to such pressures, effectively reducing their susceptibility to predation.

#### 28.2.3.3.2 Predation and Sexual Signals

Sexual signaling in fruit flies includes visual signaling, chemical signaling, and acoustic signaling (Burk 1981). Fruit fly visual sexual signals may be used agonistically between competing males or as courtship signals between the sexes. These signals include species-specific patterns that are recognition signals, postures that may communicate size, and movements such as wing waving that communicate the species, sex, and physiological state of the signaler. Some fruit flies use chemical signals as sex pheromones to attract potential mates or in courtship interactions (Fletcher and Kitching 1995; Landolt and Averill 1999; Heath et al., Chapter 29). Acoustic signals of fruit flies may be attractive to the opposite sex and the same sex, may also be important to successful courtship of males, and may be agonistic (Sivinski 1988).

28.2.3.3.2.1 Visual Signals. There are no studies specifically addressing the question of whether or not fruit flies engaged in visual signaling, such as wing waving (hamation and supination), are more susceptible to predation. Such a study would be difficult in part because such activities are associated with other behaviors that may also affect fly susceptibility, such as pheromonal and acoustic calling, and focusing attention on another fly. Regardless, one may surmise that a visually oriented predator may more easily spot a moving, rather than a stationary, prey item. Vertebrate predators such as lizards and frogs do respond to movement and are less apt or unable to recognize stationary prey (e.g., Cott 1940).

28.2.3.3.2.2 Chemical Signals. Signaling with sex pheromones by insects may entail risks, by attracting predators (Vite and Williamson 1970) and parasitoids (Sternlicht 1973; Kennedy 1979; Aldrich et al. 1987; 1991). A well-documented example of this is that of Hendrichs et al. (1994) showing that German wasps respond to the male-produced pheromone of the Mediterranean fruit fly, locate pheromonally-calling males, and that calling males suffered a higher rate of predation than noncalling males and females.

Chemical communication is generally considered to be a fairly secure mode of signaling because of the typically small quantities released, hence the predominance of pheromonal calling by females in the Lepidoptera (Thornhill and Alcock 1983). However, the susceptibility of pheromone-releasing fruit flies to predation may be exacerbated relative to that of moths by two factors. First, the male-produced pheromones of tephritid fruit flies are generally released at rates that are orders of magnitude larger than that typical found for female-produced pheromones of nocturnal Lepidoptera, although the data sets for both groups are limited. For example, the female pheromone of the tobacco budworm moth *Helicoverpa virescens* (Fabricius) is released at about 1 n/h (Teal et al. 1986) while the male pheromone of the Mediterranean fruit fly is released at about 1 µg/h (Heath et al. 1991). A much greater amount of pheromone released may increase the likelihood of a predator being able to perceive the pheromone at a distance. Second, fruit flies are predominantly diurnal while moths are predominately nocturnal, making pheromone-releasing fruit flies more vulnerable



to many groups of predators, such as predatory wasps and flies, Odonata, salticid spiders, lizards, and birds. Nocturnal predators might include bats, some web-spinning spiders, and frogs.

**28.2.3.3.2.3 Acoustic Signals.** There are as yet no indications that the acoustic signals of fruit flies, such as those of *A. suspensa* and *C. capitata*, are detectable by potential fruit fly predators or confer any additional risk on the signaler. There are examples, however, in other insects of vertebrate predator, and both invertebrate predator and parasitoid, utilization of prey acoustic signaling (Walker 1964; Cade 1975; Burk 1982). Perhaps this possibility should be kept in mind for future study of predator and parasite responses to fruit fly acoustic signals.

#### **28.2.3.3.3 Predation and Encounter Sites**

Sexual rendezvous sites of fruit flies are generally the host fruit, foliage of host trees, or foliage of nonhost plants (see Sivinski, Section 28.2.1.1). When these mating sites are on fruit, they are considered to be resource-related, with the fruit being both an oviposition substrate for females and a source of food for adult fruit flies. The use of foliage away from fruit as a mating site is often considered a lek, whether on or off trees that contain host fruit suitable for oviposition or feeding.

**28.2.3.3.3.1 Resource-related Station Taking.** The use of fruit as a mating site clearly involves males searching for females at a resource (the fruit as oviposition substrates and adult food sources). Males may perch at and call from fruit, and defend fruit from other males as territories. Courtship interactions and mating may then take place on the fruit. For example, a mating strategy of *R. pomonella* is to encounter the opposite sex and mate on the host fruit. Fruit flies on fruit generally are more exposed and susceptible to predators, and fruit flies in foliage are more hidden from view and may be more difficult for certain types of predators to find. It also seems possible that the chemical odors of fruit, particularly fruit that is damaged, may attract predators, increasing the risk of using such sites for mating. For example, vespids, potential predators of fruit flies, are attracted to and feed on many types of fruit to obtain carbohydrates.

**28.2.3.3.3.2 Leks.** A number of polyphagous and pestiferous species of tephritids encounter potential mates in leks, which by definition are nonresource-based mating aggregations. Polyphagous tropical pest species generally use leks as mate-encounter sites. It was proposed by Hendrichs and Hendrichs (1990) that predation pressure on flies at host fruit may have driven flies to form mating aggregations, leks, on foliage and away from fruit. Although fruit flies in leks may be less exposed than flies on fruit and thus might be less vulnerable to predation, Mediterranean fruit fly males in leks are at times heavily preyed upon by German wasps that are attracted to their pheromone (Hendrichs et al. 1994). The greater amount of pheromone released by a number of males in a lek may increase their attractiveness to the wasps. Nevertheless, this theory has considerable merit for many species of fruit flies. Quantitative studies of predation pressure on flies on fruit vs. flies in leks would be illuminating.

**28.2.3.3.3.3 Signaling.** The use of particular mating strategies by some fruit fly species and not others suggests that they may be adaptations to predation pressure. Similarly, particular signal traits or characteristics used by some species and not others implies that they may be a result of predation pressure. These are discussed below.

The production and release of sex-attractant pheromones by males rather than females of Tephritidae, except in *B. oleae* (Haniotakis 1974), could be interpreted as an adaptation to predation risks involved in chemical signaling by flies during the daylight hours. It is assumed that males will be the signalers where signaling is risky or unduly expensive, or where males can control access to female-required resources, and that females will be the signalers where the risk and expenditure of resources is minimal (Thornhill and Alcock 1983). The predation suffered by

pheromone-releasing male Mediterranean fruit flies from German wasps (Hendrichs et al. 1994) supports the contention that signaling can be very dangerous.

The nature of the chemicals produced by some fruit flies suggests chemical mimicry as a possible adaptation to predation on pheromonally calling fruit flies. Alkyl pyrazines are commonly found as exocrine products of Hymenoptera, including a number of species of ants and some wasps (Blum 1981). Similar compounds are produced by several species of Tephritidae; for example, 2-methyl-6-vinylpyrazine is the male pheromone of the papaya fruit fly (Chuman et al. 1987). Other pyrazines have been found in the glands or volatiles of species of *Bactrocera* (Metcalf 1990; Fletcher and Kitching 1995) and *Anastrepha* (Heath et al., Chapter 29). *N*-3-Methylbutylacetamide is an alarm pheromone of several species of *Vespula* wasps (Vespidae) (Heath and Landolt 1988) and is found in the male odors of a number of species of *Bactrocera* (Metcalf 1990). Another class of compounds, the spiroacetals, is found in a number of species of *Bactrocera* (see reviews by Metcalf 1990; and Fletcher and Kitching 1995) and is also present in the venoms of several social wasps (Francke et al. 1979; Aldiss 1983). Olean or (1,7)-dioxaspiro-(5,5) undecane, for example, is the major component of the female-produced pheromone of *B. oleae* (Baker et al. 1980), while the wasp compounds are alkyl-1,6-dioxaspiro[4,5]decane. It is tempting to speculate that a fly smelling like a hymenopteran may be protected from some predators. Although suggestive, there are as yet no data indicating any deterrent or other protective effects of these compounds produced and emitted by fruit flies.

28.2.3.3.3.4 Mimicry. Some species of fruit flies may be visual mimics of other arthropods and may thus gain benefit from protection against some predators. Generally, it is suggested that some fruit flies may mimic spiders and others may mimic social wasps.

It was noted by Mather and Roitberg (1987) and Greene et al. (1987) that the tephritids *R. zephyria* and *Z. vittigera* resemble salticid jumping spiders. Further, it has been shown that salticid spiders avoid these flies and that the protection was derived principally from the patterns on the fly wings, which resemble spider legs when viewed from the front (Mather and Roitberg 1987; Greene et al. 1987; Whitman et al. 1988). It is concluded that these flies mimic jumping spiders and are not eaten by the spiders, which also do not prey on other salticids.

The papaya fruit fly appears to mimic social wasps and may gain some protection from predators by this mimicry. They mimic species of *Polistes* and *Mischocyttarus* in Florida and other species in Central America (Landolt 1984). They possess color patterns similar to these wasps, as well as dark shading to the fore part of the wing that is similar in appearance to the folded wing aspect of Vespidae. This species is highly exposed when sexually active and during oviposition, which occurs during daylight hours on the fruit of the tree. The fruit are located on the trunk below the foliage, making the fruit and flies particularly visible. Males perch on fruit when calling, and females are immobilized for extended periods of time while ovipositing in fruit (Landolt and Hendrichs 1983). The wasplike appearance of this fly may be of particular advantage because of its activity on exposed fruit and resultant visibility to predators. The long ovipositor of the female, an apparent adaptation to access the center of fruits for deposition of eggs (Landolt 1985), may be a preselection factor because it contributes much to the wasplike appearance of the female. However, papaya fruit flies are not immune to predation and are eaten by lizards, spiders, and other predators. Of note, is the death of a captive *Anolis* lizard that was fed female *T. curvicauda*, and subsequently died with a mass of fruit fly ovipositors lodged in and puncturing the intestine. There are also species of *Anastrepha* and *Bactrocera* with elongated ovipositors that permit the deep penetration and deposition of eggs within fruit. It remains to be determined whether these species also possess additional morphological and coloration traits that

**TABLE 28.1**  
**Mating Trophallaxis in Tephritidae**

Subfamily/Tribe	Species	Timing	Direct/ Indirect	Mating Trophallaxis Confirmed?	Ref.
<b>Phyalmiinae</b>					
Acanthonevrini	<i>Afrocneros mundus</i> (Loew)	Pre	Dir	Yes	Oldroyd 1964
	<i>Dirioxa pornia</i> (Walker)	Pre+In	Ind	Yes	Pritchard 1967
<b>Trypetinae</b>					
Toxotrypanini	<i>Anastrepha striata</i> Schiner	Pre	Dir	Yes	Aluja et al. 1993
<b>Tephritinae</b>					
Eurostini	<i>Aciurina mexicana</i> (Aczel)	Pre	Ind	Yes	Jenkins 1990
Eutretini	<i>Eutreta novaeboracensis</i> (Fitch)	Pre+In	Ind	Yes	Stoltzfus and Foote 1965
	<i>Paracantha gentilis</i> Hering	Pre	Dir	Yes	Headrick and Goeden 1990
	<i>Paracantha cultaris</i> (Coquillett)	?Pre	Dir	No	Cavender and Goeden 1988
	<i>Stenopa vulnerata</i> (Loew)	Pre+In	Ind	Yes	Novak and Foote 1975
Schistopterini	<i>Schistopterum moebiusi</i> Becker	Pre+In	Ind	Yes	Freidberg 1981
	<i>Schistopterum</i> sp.	Pre+In	Ind	Yes	Freidberg, unpublished
	<i>Eutretosoma</i> sp.	Pre+In	Ind	Yes	Freidberg, unpublished
Tephrellini	<i>Metasphenisca negeviana</i> (Freidberg)	Pre+Post	Dir	Yes	Freidberg 1997
Tephritini	<i>Euaesta festiva</i> (Loew)	Pre	Dir	No	Batra 1979
	<i>Spathulina sicula</i> Rondani	Post	Dir	Yes	Freidberg 1982
Terelliini	<i>Chaetostomella undosa</i> (Coquillett)	Post	Dir	No	Steck 1984
	<i>Chaetorellia carthami</i> Stackelberg	Post	Dir	Yes	Freidberg 1978
	<i>Chaetorellia succinea</i> (Costa)	Post	Dir	No	Freidberg 1978
	<i>Neaspilota pubescens</i> Freidberg and Mathis	Pre	Dir	?	Headrick and Goeden 1994 and personal communication
	<i>Neaspilota viridescens</i> Quisenberry	Pre	Ind	Yes	Goeden and Headrick 1992
Xyphosiini	<i>Terellia quadratula</i> (Loew)	Post	Dir	No	Freidberg 1978
	<i>Ictericaria seriata</i> (Loew)	Pre+In	Ind	Yes	Foote 1967

Abbreviations: Dir = direct; In = in-mating; Ind = indirect; Post = postmating; Pre = premating.

### 28.2.3.4 Trophallaxis

#### 28.2.3.4.1 Introduction

Mating trophallaxis constitutes an array of behaviors in which the males provide females with nuptial gifts which are then consumed. It is connected with copulation and may occur shortly before, during, or shortly after it (Freidberg 1981). Unlike the definition of trophallaxis in social insects, which is limited to the "exchange of alimentary liquid among colony members and guest organisms" (Wilson 1975), mating trophallaxis encompasses the exchange of both liquid and solid substances which may have originated from a variety of organs or even from outside the body of the donor. By this definition, cases of females cannibalizing their mates during or after insemination are instances of trophallaxis.

The study of mating trophallaxis confronts one theoretical and two practical problems. The theoretical problem focuses around the somewhat vague concept of "connected with copulation." For example, what is the longest interval of time between the two activities before the idea of association becomes invalid?

On the practical side, there are two kinds of difficulties, the first being the need to prove that a behavior that superficially appears to be mating trophallaxis does indeed involve the transfer of substances. As shown in Table 28.1, several studies describe a contact between the mouthparts of

the mates (often termed a kiss), but fail to prove that a substance has been transferred during this contact. However, to provide a comprehensive treatment of the subject such ambiguous cases are nonetheless treated here as instances of mating trophallaxis.

The second practical difficulty has to do with experimental manipulation of mating trophallaxis. Because such trophallaxis is strongly associated with copulation, any experimental interference might significantly affect both behaviors. This is especially true in the apparently more widespread cases of premating trophallaxis (see below), in which any interference in the trophallactic sequence might prevent mating and thus also preclude interpretation of the significance of the trophallaxis.

Classification of the various phenomena grouped here under the general term *mating trophallaxis* is important both for the understanding of the similarities and differences in the various manifestations of the phenomenon, and for relating this behavior to evolution and phylogeny. However, readers should be aware that the suggested classification is somewhat artificial, and that categories are not always mutually exclusive.

*Premating trophallaxis* — Trophallaxis that is initiated before copulation, although sometimes continuing through part of or even the entire sexual process.

*In-mating trophallaxis* — Trophallaxis that occurs during copulation.

*Postmating trophallaxis* — Trophallaxis that occurs after copulation (= sperm transfer) has been completed.

*Direct trophallaxis* — Trophallaxis in which the trophallactic substance is directly transferred between the mates (without being placed on an intermediate substrate).

*Indirect trophallaxis* — Trophallaxis in which the trophallactic material is transferred from the donor to an intermediate substrate before being picked up by the recipient.

*Stomodaeal trophallaxis* — Trophallaxis in which the donor secretes the trophallactic substance from its mouth.

*Proctodaeal trophallaxis* — Trophallaxis in which the donor secretes the trophallactic substance from its anus.

Mating trophallaxis, at least in Tephritidae, appears to be a relatively rare phenomenon, and has been reported for only about 20 species. Knowledge about this phenomenon is, therefore, scarce, generally anecdotal, and incomplete. Presentation of the available knowledge and continued research on this topic are undoubtedly necessary, and should result in additional discoveries of this general phenomenon.

#### 28.2.3.4.2 *Distribution in the Animal Kingdom*

Trophallaxis in vertebrates has been documented in a number of bird species (Johnston 1962). In invertebrates it is restricted to Arthropoda, and has been described in both spiders (Arachnida) and insects (Insecta). In the former, it is well known that female widow spiders devour their mates after sperm transfer is completed (Kaston 1970). In insects, the phenomenon has been reported in several orders, notably the Orthoptera (e.g., Wedell 1994), Dictyoptera (e.g., Roeder et al. 1960), Hymenoptera (e.g., Given 1953), Mecoptera (e.g., Thornhill 1976) and Diptera. In Diptera, as in Mecoptera, mating trophallaxis may occur in two distinct ways: (1) through the transfer of prey, as in Empididae (Kessel 1955); and (2) through secretions, as in Asteiidae (Freidberg 1984), Drosophilidae (Kaneshiro and Ohta 1982), Ephydriidae (Mathis and Freidberg, unpublished data), Micropezidae (Wheeler 1924), Platystomatidae (Piersol 1907), Sciomyzidae (Green 1977; Berg and Valley 1985), and Tephritidae (see Table 28.1).

#### 28.2.3.4.3 *Distribution in the Tephritidae*

Table 28.1 lists all the tephritid species in which mating trophallaxis has either been reported or is suspected to occur. Reports vary in length and depth, ranging from a few words or an illustration to entire articles devoted to the subject. Representative cases are described more fully below.

Of all the cases in Table 28.1, only a few have been described in enough detail to warrant summarizing here. Of these, the case of *Schistopterum moebiusi* Becker (Freidberg 1981) was selected as an example of premating trophallaxis because of the field observations of this species, which are generally difficult to obtain. *Spathulina sicula* Rondani (Freidberg 1982; as *S. tristis* (Loew)) was selected both because it is the only well-studied case of postmating trophallaxis, and because it is the only case combining observations with experimentation.

*Schistopterum moebiusi* is a tiny (length about 2 mm) but colorful, widespread species distributed from Israel to South Africa, whose sole known host plant is the shrub *Pluchea dioscoridis* (L.) DC. (Asteraceae). *Schistopterum moebiusi* exhibits premating, indirect, stomodeal trophallaxis. Males defend territories near inflorescences and engage in aggressive encounters with other male intruders. When a female approaches a territorial male, he receives her with the same agonistic behavior shown to a male intruder. An unreceptive female decamps by running or flying away. A receptive female remains on the same leaf, and the male continues his approach by scissoring (enanting; see Glossary, Chapter 33) his wings and partially circling the female several times, both clockwise and counterclockwise. During this activity the female either moves about or remains stationary, enanting and moving her wings slightly. This courtship behavior takes from 30 s to 2 min.

When a female stands motionless, the male extends his proboscis to the leaf surface and secretes a white, frothy material from his labella. This material builds up into a vertical pillar, with new material supplied to the top. In the last stage of secretion the male broadens the upper part of the pillar into a mushroomlike shape, and by applying pressure to it, tilts it to one side. The final height of the structure is about 1 mm, and its white color makes it conspicuous against the green background. During secretion of the froth, which lasts 10 to 50 s, the female faces the scene from a distance of usually less than 10 mm, mostly 1 to 2 mm. Her occasional attempts to approach the froth are stopped by enanting activity by the male. When secretion is completed, the male backs away a short distance. If the female is facing him, she immediately approaches, extrudes her proboscis, and feeds on the froth. While she is feeding, he mounts her. If the female is not facing the male, or stands farther away, the male circles her and, while enanting, he orients her toward the froth. In the latter case, either the female begins feeding, or the male first adds more froth on top of the pillar. If the female does not feed, the male may add froth a second or even a third time, until the female either begins to feed or decamps. A feeding female extends her aculeus, which is immediately grasped by the male's surstyli. The period from terminating secretion to establishing genital contact lasts only a few seconds. Copulation posture is generally similar to that of many other observed species, but with the aculeus greatly extruded, possibly its whole length. Froth feeding and copulation sometimes proceed uninterrupted, until the female has finished the froth or for several seconds thereafter. Such copulations last 3 to 5 min.

If the male dismounts from the female shortly before she has finished feeding, he usually stays close to her, or enantes nearby, but without trying to resume copulation. The female continues to feed on the froth until nothing is left (up to 1 more minute). In many instances the male dismounts while the female is still feeding, but behaves in a different manner: 2.5 to 4 min after onset of copulation the male dismounts backward, circles the female and what is left of the froth, and faces both, so that the froth is located between them. He then resumes secretion and reconstructs the froth, while the female, who has stopped feeding, continues to face him. The behavior of the couple during froth reconstruction is similar to that during the initial formation of the froth. This includes attempts at feeding by the female and preventative actions by the male. In one case, however, a female was observed feeding from one side of the froth head, while the male was busy reconstructing it at the other. After reconstruction the male mounts the female as described before, thus performing a "set" of sequential copulations. Such a "set" is composed of several alternating copulations and reconstructions. The male fully reconstructs the froth each time, or even enlarges it beyond its original dimensions, an action that requires 10 to 45 s. In one extreme case we observed five reconstructions in one "set" of copulations that lasted more than 24 min. Abandoned froth pillars and feeding on froth by flies other than the original female were occasionally observed.

Premating trophallaxis is the most widespread kind of mating trophallaxis in Tephritidae, and Freidberg (1981) compared the details of the behavior described above with those of four other species: *Stenopa vulnerata* (Loew), *Ictericaria seriata* (Loew), *Eutreta novaeboracensis* (Fitch) (as *E. sparsa* (Wiedemann)), and *Dirioxa pornia* (Walker), all exhibiting indirect, premating trophallaxis. However, additional cases of similar behaviors have since been reported (e.g., Jenkins 1990) or observed (in *Schistopterum* sp. and *Eutretosoma* sp.; Freidberg, unpublished data). It is important to stress that in all the species that exhibit indirect trophallaxis, copulation does not take place without mating trophallaxis.

Postmating trophallaxis has so far been reported for only a few species of Tephritidae, of which *Spathulina sicula* was the subject of the most-detailed study (Figure 10\*). This species is a moderately small (3 to 4 mm long), blackish fly, with a reticulate wing pattern and a nearly circum-Mediterranean distribution. It induces the formation of terminal stem galls on three species of *Phagnalon* (Asteraceae) (Persson 1976). *Spathulina sicula* exhibits direct, stomodeal, postmating trophallaxis. Its reproductive behavior was primarily studied in the laboratory, where single males and females were placed together in petri dishes. Males initiate courtship and are usually successful in achieving copulation within 1 to 30 min after introduction, although coupling occasionally begins 2 h after introduction, or does not occur at all. The average duration of 105 copulations was  $3.06 \pm 0.05$  h (range: 1:07 to 5:16). The male occasionally enanates (scissors) shortly before dismounting the female, then releases the female's aculeus, dismounts her by stepping slowly backward, and stands still very close to the female.

The association between the sexes was seldom immediately broken at dismounting. In more than 90% of the observed copulations this was only the beginning of postmating behavior. Sometimes one or both partners may engage in self-cleaning and grooming for several minutes, and they may also walk around. However, usually within a few seconds after the male dismounts, the female will turn and face him. Her proboscis is extended and moves as if the labella are "searching" for those of the male. Within a few seconds she finds his proboscis, and when matched in a "kissing" posture (Figure 10\*), a milk-white fluid appears between the labella of the two flies. Body position during this stage is oblique to the substrate, the male somewhat more erect, so that the female's head is a little lower than the male's. During the "kiss" the female's proboscis is more active than that of the male, while strong constrictions can be observed in the male's abdomen. White fluid continuously appears between the labella, and when the behavior is observed in correct illumination under the stereoscopic microscope, this fluid seems to enter the food canal of the female's proboscis. The "kiss" may last several minutes ( $5 \text{ min } 19 \text{ s} \pm 0 \text{ min } 23 \text{ s}$ ,  $n = 51$ ; range: 1 min 10 s to 13 min 36 s), and is often interrupted by one or several short intervals, during which the labella of the partners lose contact. The male seems to break the "kiss" more frequently, and males were often observed trying to withdraw while their labella were still attached to those of the female, in some cases by pushing at the female's head with their forelegs. Sometimes, they eventually succeeded in releasing themselves, but often they seemed to give up the struggle and continued "kissing." Initiation of grooming activity, particularly of the genitalia, may occur even before the labella of the partners finally detach.

Most other known cases of mating trophallaxis in tephritidae are generally rather similar to the two cases described above. There are, however, two notable exceptions. The first is the case of *N. viridescens* (Goeden and Headrick 1992), which is the only tephritid to exhibit proctodeal (in addition to stomodeal) trophallaxis. The second exceptional case is that of *Metasphenisca negeviana* (Freidberg), the only species to exhibit both premating and postmating trophallaxis (Freidberg 1997).

#### 28.2.3.4.4 Anatomy, Ultrastructure, and Biochemistry

It has been suggested that the male's salivary glands are the source of the trophallactic substance in at least some Tephritidae, although Jenkins (1990) deduced that contents of the crop contributed

\* Figure 10 follows p. 204.

to the nuptial gift of *Aciurina mexicana* (Aczél). Freidberg (1982) described the sexually dimorphic salivary glands of *S. sicula*. In this species the sacs of the male glands are much larger than those of the female and contain a milky substance, whereas those of the female are translucent. Freidberg (1978) also described the strikingly sexually dimorphic salivary glands in several species of Terebrantini, most of which were observed to perform postmating trophallaxis. However, a somewhat similar sexual dimorphism also occurs in *Anastrepha suspensa* (Nation 1974), a species that does not practice mating trophallaxis and in which the large male glands are associated with pheromone production. Pritchard (1967) showed different staining reaction in male and female salivary glands of *Dirioxa pornia*, and Freidberg (1982) gave circumstantial evidence that the milky substance produced and stored in the male salivary glands of *S. sicula* is transferred and ingested by the female during the “kiss.” Freidberg (1978) showed that this “milk” is an emulsion containing tiny round particles (diameter about 1.5  $\mu\text{m}$ ), each with a concentric design. Preliminary biochemical tests of the “milk” detected high absorption at 280 to 290  $\mu\text{m}$ . The molecular weight of most of the material was less than 10,000 D. Tests for amino acids and sugars were indecisive (Freidberg 1978), and additional tests, using more-modern techniques, should be employed to reevaluate these findings.

#### 28.2.3.4.5 Experiments

Experiments designed to reveal the potential benefits that might accrue to females receiving trophallactic substances should be based primarily on artificial prevention of trophallaxis. However, it may be difficult to draw conclusions from such experiments, especially in cases of premating trophallaxis, in which prevention of trophallaxis results in no copulation.

In contrast, experimentation on postmating trophallaxis is possible, and *S. sicula* provides a suitable model for such experiments. Freidberg (1982) used this species for testing the effect of trophallaxis on subsequent female sexual receptivity, longevity, and fecundity, and on female fertility and progeny success. The basic design of the experiments consisted of a comparison of a test group of females that copulated, but were separated from their mates before “kissing,” with a control group of mated females that were allowed to “kiss.” The females were not given food prior to the experiment.

After nine days neither “kissed” nor “unkissed” females mated a second time, so that any inhibitive factor was transferred/communicated during copulation, and not through trophallaxis. Differences in longevity and fecundity between the test and control group were not statistically significant. The effect of trophallaxis on fertility was only studied qualitatively, and offspring were recovered from developing galls induced by “unkissed” females.

#### 28.2.3.4.6 Evolutionary Implications and Phylogeny

Premating trophallaxis is a prerequisite for copulation, whereas postmating trophallaxis is not. Premating trophallaxis could be the result of sexual selection (see Darwin 1871); that is, males compete through their ability to produce and guard nuptial gifts (such as a mound of froth), and females use these behaviors and substances to choose mates from among their suitors. It is possible that these nuptial gifts are either valuable resources or chemical displays whose content is informational rather than nutritional. However, perhaps postmating trophallactic substances would be more likely to consist solely of male resources that enhance the fecundity or longevity of his mate (despite the present lack of experimental evidence of this male investment). After all, females have already copulated, and the opportunity to choose a mate has passed — or has it? An alternative view has been suggested by Eberhard (1994), who argued that courtship, including nuptial giving, may persist during, or even following, copulation. This entails “cryptic” (in the sense of internal, difficult to observe) female choice. If so, then it is possible that postmating trophallaxis somehow acts to influence females to employ the sperm of a particular male in the fertilization of her eggs. However, the absence of multiple matings in female *S. sicula*, the best-studied case of postcopulatory



trophallaxis, makes it unlikely that there is an opportunity to perform cryptic mate choice in at least this instance.

All tephritid species practicing mating trophallaxis are listed in Table 28.1. The resulting inventory is obviously insufficient for cladistic analysis. Nevertheless, we would like to highlight two points: (1) mating trophallaxis has been definitely reported in the most primitive (Acanthonevrini) as well as the most derived (Tephritini) tribes of Tephritidae; (2) most cases have been reported in the Tephritinae, the most-derived subfamily, and these instances occur in no fewer than eight tribes. This may mean that the phenomenon is much more widespread than previously thought, and it would appear to have evolved independently many times within the family.

#### 28.2.3.5 Copulation Duration — Sperm Competition and Female Choice

The genus *Anastrepha* is one of the best-studied groups with respect to copulation duration. As described by Aluja et al. (Chapter 15), mean mating times vary from  $24.3 \pm 1.5$  min in *A. bistrigata* to  $350 \pm 60$  min in *A. hamata*. It is noteworthy that three of the species with the longest mating times are also among the larger species.

Why is there so much variability among species? Couplings that extend beyond what is required for sperm transfer in related species are often interpreted in terms of sperm competition avoidance (Parker 1970), protection from predators (Sivinski 1981), or “cryptic female choice,” that is, courtship that continues through mating and influences the female to retain or utilize the sperm of the signaling male preferentially (Eberhard 1996; Belford and Jenkins 1998.) There are also instances that are seemingly inconsistent with mate guarding to avoid sperm competition. For example, *A. leptozona* Hendel form relatively long unions (>6 h), but these continue into the night, beyond the sexual signaling period, and presumably when no other males would be searching for mates. Couplings by *Euaestoides acutangulus* are even longer and those initiated at midday extend into the following afternoon (Headrick and Goeden 1994). This does not discount the possibility that males use this time to transfer materials that might induce refractory periods and thereby protect their ejaculates. However, in some species (e.g., *A. suspensa*), females appear to have considerable control over mating durations; because males have a difficult time maintaining their position when females become restless and move about. Males respond by producing what appear to be brief repetitions of “precopulatory song,” an important acoustic courtship signal (see Aluja et al., Chapter 15). If long copulations are performed with the compliance of the female, it may be more likely that the male is either protecting its mate (and the mother of their offspring) from predators, or is continuing to provide the female with information she will use to make reproductive decisions (see Eberhard, Chapter 18; Belford and Jenkins 1998).

Materials other than refractory-period inducers, such as nutrients and defensive compounds, may also be transferred by males in their ejaculates, and the mechanics of these transfers might also influence copulation durations (e.g., Gwynne 1983). In several Diptera species males provide resources that are incorporated into female somatic tissue and developing ovaries (e.g., Markow and Ankney 1984). In *Drosophila pseudoobscura* Fralova multiple-mated females have greater fertility, suggesting that they have acquired multiple male “investments” (Turner and Anderson 1983). Radioactively labeled substances in the ejaculate of *A. suspensa* were later recovered in the unfertilized eggs and tissues of mated females (Sivinski and Smittle 1987). However, the amounts of these substances appear to be small, and are perhaps inconsequential as male investments.

### 28.3 THE PHYLETIC DISTRIBUTION OF SEXUAL BEHAVIORS

Information is presented in an annotated table (Table 28.2).

**TABLE 28.2**  
**Phyletic Distribution of Sexual Behaviors**

Taxa	Behavior							
	Life-History Strategy		Wing Displays		Asynchronous	Synchronous	Pleural	
	Aggregative	Circumnatal	Hamation	Enantion	Supination	Supination	Lofting	Distention
<b>Subfamily Blepharoneurinae</b>								
<i>Blepharoneura</i>								
<i>atomaria</i>	Y	N	Y	Y	Y	Y	Y	U
<i>manchesteri</i>	Y	N	Y	Y	Y	Y	U	U
<i>perkinsi</i>	Y	N	Y	Y	Y	Y	U	U
<b>Subfamily Phytalmiinae</b>								
<b>Tribe Phytalmiini</b>								
<i>Phytalmia</i>								
<i>alcicornis</i>	Y	N	N	Y	N	U	Y	Y
<i>cervicornis</i>	Y	N	N	U	U	U	Y	Y
<i>mouldsi</i>	Y	N	N	Y	N	Y	Y	Y
<b>Subfamily Dacinae</b>								
<b>Tribe Ceratitidini</b>								
<i>Ceratitis</i>								
<i>capitata</i>	Y	N	U	Y	U	Y	U	Y
<b>Tribe Dacini</b>								
<i>Bactrocera</i>								
<i>dorsalis</i>	Y	N	U	U	U	U	U	U
<i>oleae</i>	Y	N	U	U	U	U	U	Y
<i>tryoni</i>	Y	N	U	U	U	U	U	Y
<b>Subfamily Trypetinae</b>								
<b>Tribe Carpomyini</b>								
<i>Rhagoletis</i>								
<i>cresoni</i>	Y	N	N	Y	N	N	Y	Y
<i>indifferens</i>	Y	N	U	Y	U	Y	Y	U
<i>pomonella</i>	Y	N	U	Y	U	U	U	Y
<b>Tribe Toxotrypanini</b>								
<i>Anastrepha</i>								
<i>bistrigata</i>	Y	N	U	U	U	Y	U	Y
<i>fraterculus</i>	Y	N	U	U	U	Y	U	Y
<i>ludens</i>	Y	N	U	U	U	Y	U	Y
<i>obliqua</i>	Y	N	U	U	U	Y	U	Y
<i>pseudoparallela</i>	Y	N	U	U	U	Y	U	Y
<i>sororcula</i>	Y	N	U	U	U	Y	U	Y
<i>suspensa</i>	Y	N	U	U	Y	Y	U	Y
<i>striata</i>	Y	N	U	Y	U	Y	Y	Y
<i>Toxotrypana</i>								
<i>curvicauda</i>	Y	N	U	Y	U	U	U	Y
<b>Tribe Trypetini</b>								
<i>Euleia</i>								
<i>fratria</i>	U	U	Y	Y	U	Y	U	U

[illegible]

**TABLE 28.2 (continued)**  
**Phyletic Distribution of Sexual Behaviors**

Taxa	Behavior							
	Life-History Strategy		Wing Displays		Asynchronous	Synchronous	Pleural	
	Aggregative	Circumnatal	Hamation	Enantion	Supination	Supination	Lofting	Distention
<b>Subfamily Tephritinae</b>								
<b>Tribe Acrotaeniini</b>								
<i>Tomoplagia</i>								
<i>cressoni</i>	Y	N	U	Y	Y	U	U	Y
<b>Tribe Cecidocharini</b>								
<i>Procecidochares</i>								
<i>anthracina</i>	N	Y	N	Y	N	Y	N	N
<i>flavipes</i>	Y	N	Y	Y	N	U	N	N
<i>kristinae</i>	N	Y	N	Y	N	U	N	N
<i>lisae</i>	N	Y	N	Y	N	U	N	N
<i>minuta</i>	N	Y	N	Y	N	U	N	N
sp. nr. <i>minuta</i> (NM)	Y	N	U	Y	U	U	N	U
<i>stonei</i>	N	Y	N	Y	Y	U	N	N
<b>Tribe Eurostini</b>								
<i>Aciurina</i>								
<i>ferruginea</i>	N	Y	Y	U	Y	Y	N	U
<i>mexicana</i>	Y	N	Y	U	Y	Y	N	Y
<i>thoracica</i>	Y	N	Y	N	Y	Y	N	Y
<i>trixa</i>	N	Y	Y	N	Y	Y	N	U
<i>Eurosta</i>								
<i>comma</i>	Y	N	U	Y	U	U	U	U
<i>Valentibulla</i>								
<i>californica</i>	N	Y	U	U	Y	Y	U	U
<i>dodsoni</i>	N	Y	N	U	Y	Y	U	U
<b>Tribe Eutretini</b>								
<i>Eutreta</i>								
<i>angusta</i>	N	Y	Y	N	Y	Y	U	U
<i>diana</i>	N	Y	Y	N	Y	Y	U	U
<i>Paracantha</i>								
<i>cultaris</i>	Y	N	Y	N	Y	Y	N	Y
<i>gentilis</i>	Y	N	Y	N	Y	Y	N	Y
<i>Stenopa</i>								
<i>vulnerata</i>	Y	N	U	U	Y	U	U	U
<b>Tribe Myopitini</b>								
<i>Goedenia</i>								
<i>formosa</i>	Y	N	Y	N	N	N	U	Y
<i>timberlakei</i>	Y	N	Y	N	N	N	U	Y
<i>species</i>	Y	N	Y	N	N	Y	U	Y
<i>Urophora</i>								
<i>affinis</i>	Y	N	U	Y	U	Y	U	U
<i>quadrifasciata</i>	Y	N	U	Y	U	Y	U	U

[illegible]

**TABLE 28.2 (continued)**  
**Phyletic Distribution of Sexual Behaviors**

Taxa	Behavior							
	Life-History Strategy		Wing Displays		Asynchronous	Synchronous	Pleural	
	Aggregative	Circumnatal	Hamation	Enantion	Supination	Supination	Lofting	Distention
<b>Tribe Noetini</b>								
<i>Xenochaeta</i>								
<i>dichromata</i>	Y	N	U	U	Y	Y	U	U
<b>Tribe Schistopterini</b>								
<i>Schistopterum</i>								
<i>moebiusi</i>	Y	N	Y	U	U	U	U	U
<b>Tribe Tephritini</b>								
<b><i>Campiglossa</i> genus group</b>								
<i>Campiglossa</i>								
<i>genalis</i>	Y	N	Y	N	Y	Y	Y	Y
<i>murina</i>	Y	N	Y	N	Y	Y	Y	Y
<i>sabroskyi</i>	Y	N	U	N	Y	U	Y	Y
<i>steyskali</i>	Y	N	Y	N	Y	U	Y	Y
<i>variabilis</i>	Y	N	Y	N	Y	Y	Y	Y
<i>Dioxyna</i>								
<i>picciola</i>	Y	N	Y	N	Y	U	Y	Y
<b><i>Euarestoides</i> genus group</b>								
<i>Euarestoides</i>								
<i>acutangulus</i>	Y	N	Y	Y	Y	U	U	Y
<i>flavus</i>	Y	N	Y	U	Y	U	U	U
<b><i>Tephritis</i> genus group</b>								
<i>Tephritis</i>								
<i>araneosa</i>	Y	N	Y	Y	Y	Y	N	Y
<i>arizonaensis</i>	Y	N	Y	Y	Y	U	U	Y
<i>dilacerata</i>	Y	N	U	U	Y	U	U	U
<i>stigmatica</i>	Y	Y	Y	Y	Y	Y	Y	Y
<i>Neotephritis</i>								
<i>finalis</i>	Y	N	Y	N	Y	Y	U	Y
<i>Trupanea</i>								
<i>actinobola</i>	Y	N	Y	N	Y	Y	N	Y
<i>arizonaensis</i>	Y	N	Y	N	Y	Y	N	Y
<i>californica</i>	Y	N	Y	N	Y	Y	N	Y
<i>conjuncta</i>	Y	N	Y	N	Y	U	U	U
<i>imperfecta</i>	Y	N	Y	N	Y	U	U	U
<i>jonesi</i>	Y	N	Y	N	Y	Y	U	Y
<i>nigricornis</i>	Y	N	Y	N	Y	Y	U	Y
<i>radifera</i>	Y	N	Y	N	Y	Y	U	Y
<i>signata</i>	Y	N	Y	N	Y	Y	U	Y
<i>wheeleri</i>	Y	N	Y	N	Y	Y	U	Y
<b><i>Tephritini Incertae Sedis</i></b>								
<i>Euaresta</i>								
<i>bella</i>	Y	N	U	U	Y	Y	U	U
<i>festiva</i>	Y	N	U	U	Y	Y	U	U
<i>stigmatica</i>	Y	N	Y	Y	Y	Y	Y	Y

Behavior										
Mouthpart Extension	Labellar Wagging	Trophallaxis	Foreleg Extension	Midleg Abduction	Side Step	Male Stalking	Mate Guarding	Resource Guarding	Multiple Matings	Copulation Duration
U	U	U	U	U	Y	Y	U	U	Y	1.5 h
Y	U	Y	Y	U	Y	U	U	Y	U	U
Y	Y	U	Y	U	Y	N	Y	U	Y	4 h
Y	Y	U	Y	U	U	N	U	U	U	2 h
Y	Y	U	U	U	U	N	U	U	U	5 h
Y	Y	U	Y	U	U	N	U	U	U	5 h
Y	Y	U	Y	U	U	N	U	U	U	4.6 h
Y	Y	U	Y	U	U	N	Y	U	Y	1 (36) h
U	U	U	U	U	U	Y	Y	Y	Y	24 h
U	U	U	U	U	Y	Y	U	U	U	2 h
U	U	U	Y	U	U	Y	U	U		
U	U	U	Y	U	U	Y	U	U	U	2.5–8 h
U	U	U	U	U	U	Y	U	U	Y	>1 h
Y	U	U	Y	U	U	Y	U	U	U	2–12.5 h
U	U	U	U	U	U	Y	U	U	U	4 h
U	U	U	Y	U	U	Y	U	U	U	0.08 h
U	U	U	U	U	U	Y	U	U	U	U
U	U	U	Y	U	U	Y	U	U	U	U
U	U	U	U	U	U	U	U	U	U	U
U	U	U	U	U	U	U	U	U	U	U
U	U	U	Y	U	U	Y	U	U	U	0.17 h
U	U	U	Y	U	U	Y	U	U	U	0.1 h
U	U	U	U	U	U	Y	U	U	U	U
U	U	U	U	U	U	Y	U	U	U	U
U	U	U	U	U	U	Y	U	U	U	0.08 h
Y	U	U	U	U	U	U	U	U	U	0.3–1 h
Y	U	U	U	U	U	U	U	U	U	0.3–1 h
Y	Y	N	Y	Y	Y	N	N	U	U	1 h



**TABLE 28.2 (continued)**  
**Phyletic Distribution of Sexual Behaviors**

Taxa	Behavior							
	Life-History Strategy		Wing Displays		Asynchronous	Synchronous	Pleural	
	Aggregative	Circumnatal	Hamation	Enantion	Supination	Supination	Lofting	Distention
<b>Tribe Terelliini</b>								
<i>Chaetostomella</i>								
<i>undosa</i>	Y	N	U	Y	U	U	U	U
<i>Neaspilota</i>								
<i>achilleae</i>	Y	N	Y	N	N	N	N	Y
<i>callistigma</i>	Y	N	Y	N	N	N	N	Y
<i>viridescens</i>	Y	N	Y	N	N	N	N	Y
<b>Tribe Xyphosiini</b>								
<i>Icterica</i>								
<i>circinata</i>	Y	N	U	U	Y	Y	U	U
<i>seriata</i>	Y	N	U	U	Y	Y	U	U

Key: Y = confirmed; U = unobserved; N = does not occur.

## 28.4 PHYLOGENY AND BEHAVIOR

### 28.4.1 SEXUAL SELECTION AND SPECIATION

In his book *Modes of Speciation*, White (1978) states that “the comparative study of speciation, in relation to the population structure and genetic architecture of living organisms, is assuming an increasing importance in evolutionary studies.” In a volume titled *Mechanisms of Speciation*, Mayr (1982) contributed an article in which he stated, “Speciation ... now appears as the key problem of evolution. It is remarkable how many problems of evolution cannot be fully understood until Speciation is understood.”

Within the last decade there has been renewed interest in the process of speciation, as evidenced by two edited volumes on the topic (Otte and Endler 1989; Lambert and Spenser 1995). Otte and Endler (1989) in their preface state that the collection of papers “illustrates the inhomogeneity among diverse taxa in their patterns and processes of speciation” and “[w]e hope that this will encourage reassessment of both data and theory at all levels, and ultimately contribute to a new synthesis of evolutionary ideas.” These thoughts by some of the leading researchers in speciation provide the primary thesis of this section, especially the hope that studies of speciation will lead to new ideas regarding evolutionary processes.

It is a generally accepted notion that the accumulation of genetic differences that result in reproductive isolation between daughter populations is the most important feature of the speciation process and, as such, has been the primary focus of attention in research on speciation. One school of thought is that isolation barriers arise as incidental by-products of natural selection during spatial isolation rather than as a direct result of selection for reproductive isolation (Muller 1942; Mayr 1963). Others believe that genetic barriers formed during allopatry are incomplete and that isolation is perfected following secondary contact of the daughter populations (Fisher 1930; Dobzhansky 1940). In the latter, it is suggested that some form of intrinsic barriers such as hybrid inferiority arise as a result of natural selection during allopatry and that selection acts against those parental genotypes that hybridize. Thus, hybridization actually strengthens interspecific isolation barriers, and premating barriers such as behavioral and ecological differences evolve as a response to natural selection against hybridization.

			Behavior							
Mouthpart Extension	Labellar Wagging	Trophallaxis	Foreleg Extension	Midleg Abduction	Side Step	Male Stalking	Mate Guarding	Resource Guarding	Multiple Matings	Copulation Duration
Y	U	U	U	U	U	U	U	U	U	2.5 h
U	U	U	U	U	Y	Y	U	U	U	3 h
U	U	U	Y	U	Y	Y	U	U	U	U
Y	U	Y	Y	U	Y	Y	Y	Y	Y	3 to 9 h
Y	U	U	U	U	U	U	U	U	U	U
U	U	Y	U	U	U	U	U	Y	Y	1–3 h

Based on the results of some of his earlier studies on the mating behavior of Hawaiian *Drosophila*, Kaneshiro (1989) concluded that "sexual selection may be a pivotal feature of the speciation process and may indeed play a prominent role in the origin of new species." For nearly a century, the role of sexual selection as an important factor in the speciation process has been largely ignored by evolutionary biologists. Even Darwin (1871), despite his strong convictions "of the power of sexual selection" noted that "sexual selection will also be dominated by natural selection." Only within the past two decades has there been renewed interest in investigating sexual selection and its influence on the "mutual adjustment of the sexes to what may be called the intraspecific sexual environments" (Carson 1978). Researchers began to focus on changes within the sexual environment as a major component of genetic adaptations during speciation (Lande 1981; 1982; Kirkpatrick 1982).

One of the classical theories of sexual selection is the notion that female choice and male character would coevolve very rapidly (i.e., "runaway selection") within an interbreeding population (Fisher 1930; O'Donald 1977; 1980). Lande (1981; 1982) developed polygenic models to confirm the runaway process of Fisher's original ideas. In all these models, it is assumed that two factors act to counterbalance the runaway process of sexual selection. On the one hand, female preference for a certain male trait acts to select for elaborate forms of that trait. On the other hand, natural selection acts to maintain the optimum male phenotype to survive in a particular environment. Thus, an essential component of the classical sexual selection model is the role of natural selection in checking the runaway process that results from the genetic correlation between male trait and female preference for that trait.

It is theorized that directional selection via female choice for males with an exaggerated secondary sexual character is counterbalanced by the forces of natural selection due to the reduced survivability of males with excessive adornments. Eventually, when the genetic variability for the upper limits of the exaggerated character is reduced to the point where selection can no longer produce males with structures detrimental to their survival, the optimum phenotype becomes fixed in the population. This is a paradox inherent in the runaway sexual selection model. The reduction in variability for a male trait means that there can no longer be selection for such traits. Does this mean that secondary sexual characters that appear to be used in some aspect of the mating system, whether intrasexual competition among males or in epigamic selection, are not under direct sexual selection?

To address the issue of reduced genetic variability inherent in the runaway model, Kaneshiro (1989) proposed an alternative sexual selection model. Based on mating studies of Hawaiian *Drosophila*, Kaneshiro (1976; 1980; 1983; 1987) suggested that there is a range of mating types segregating in the two sexes; that is, males that are highly successful in mating and females that are very choosy at one end of the distribution, with males that are not so successful and females that are not so choosy at the other end. Data from mate-choice experiments conducted in the laboratory, as well as observations of courtship encounters in the field, suggest that the most likely mating within an interbreeding population occurred between males with exceptional mating qualities and females that were nonchoosy. Observations of mating experiments in the laboratory indicate that in most cases, successful matings occurred very quickly, within a few seconds following initial encounter between a male and female. In many cases, although the male may perform courtship displays vigorously for a long period, the female will continue to reject the male's attempt to copulate. In the field, where numerous observations of courtship attempts have been observed (K. Kaneshiro and P. Conant, unpublished data), more than 90% result in the female rejecting and decamping from the male's territory. In the few cases where a courtship encounter resulted in successful copulation, the female appeared to accept the male after an extremely brief courtship display (i.e., within a few seconds). In all of the observations where courtship lasted for more than 15 s, the female inevitably decamped from the male's mating territory even if the male continued to court for several minutes. A possible explanation for these observations is that in cases where a female rejects the male even after a lengthy courtship display, either the female is very choosy or the male does not have the courtship ability to satisfy the requirements of most such females in the population. On the other hand, those cases that result in successful copulation after a very brief courtship display by the male would appear to be between males that are highly successful in mating ability and females that are not so choosy.

It was also hypothesized that there is a strong genetic correlation between male mating ability and female choosiness (Kaneshiro 1989). Some preliminary selection experiments for these two behavioral phenotypes in the two sexes provide some support for this hypothesis. Kaneshiro (1989) conducted selection experiments in a Hawaiian *Drosophila* species in which males assayed for high mating success were crossed with females assayed for high choosiness. Within a single generation of selection, the sons of such mating pairs displayed mating ability similar to their fathers and the daughters displayed choosiness similar to their mothers. Similarly, strains with the opposite phenotype, that is, poor male mating ability and nonchoosy females, could be selected with significant results even after a single generation of selection. The results of these experiments indicate that by selecting both behavioral phenotypes in the two sexes simultaneously, it was possible to obtain strains with males and females that resembled the mating behavioral qualities of their parents even within a single generation.

Thus, matings in the natural population between highly successful males and less choosy females and the strong genetic correlation between these behavioral phenotypes in the two sexes would maintain the entire range of mating types in both sexes. Consequently, with this model, in contrast to the runaway selection model, levels of genetic variability of any phenotypic trait involved in mating success would be maintained rather than reduced as predicted by the runaway model. Rather than natural selection acting to counterbalance the directional runaway selection as seen in the classical models of sexual selection, the model proposed by Kaneshiro views sexual selection acting by itself to maintain a balanced polymorphism of the mating system.

Kaneshiro (1989) further extended his ideas on sexual selection to its role in the speciation process. During periods when population size is small, such as might be expected when a subset of the parent population is isolated by some extrinsic (spatial) barrier, there is a strong selection for less choosy females in the population. Under these conditions, females that are choosy may never encounter males able to satisfy their courtship requirements. Within a few generations of small population size, there will be an increase in frequency of less choosy females in the population with a corresponding shift in gene frequencies toward the genotypes of these females. This is further accompanied by a destabilization of the coadapted genetic system resulting in the generation of

novel genetic recombinants, some of which may be better adapted to the new habitat of the daughter population. Those recombinants that are closely linked or correlated with the genotypes of the less choosy females will be strongly selected and can spread quickly throughout the population. Thus, the dynamics of the sexual selection process permit the population to overcome any effects of such drastic reduction in population size and even to recover from the genetic disorganization that accompany such population events. In rebuilding its coadapted genetic system as the population size increases, selection may result in a shift toward a new adaptive peak, which may include reproductive barriers that isolate the incipient population from the parental population. Thus, sexual selection is viewed as playing an extremely important role in the initial stages of species formation and providing a mechanism for generating novel genetic material with which the population can continue to respond to sexual as well as natural selection in completing the speciation process.

#### **28.4.2 MATING BEHAVIOR AND THE RECONSTRUCTION OF PHYLOGENY**

Sexual behaviors in tephritids are many and diverse, and thus form a rich pool of candidate characters for phylogenetic analyses. However, their use will depend on the resolution of homology or homoplasy and the level of taxonomic analysis chosen. Pinto (1977), in his seminal work on meloid sexual behavior, stated that a rich diversity of behaviors does not translate into optimal taxonomic utility. For higher level classifications, the behaviors would have had to diverge early in the group's evolution and progress accordingly through time. Behaviors that achieve high levels of divergence in the group's recent history are thus restricted in phylogenetic value to lower-ranked taxa.

Sexual characters represent only one facet of an animal's behavior and may be on a par with any other generalized behavioral grouping such as oviposition, grooming, or feeding. Similarly, sexual behavior may also be on a par with other phenotypic expressions such as the products of behavior (nests, galls, spermatophores, and webs) or interspecific interactions (host finding and resource utilization) that have had previous phylogenetic utility (Wenzel 1992). The following will explore levels of taxonomic resolution and homology regarding tephritid sexual behavior.

##### **28.4.2.1 Homology and Homoplasy**

Behavioral characters are rarely used in the development of phylogenetic reconstructions (Sanderson et al. 1993); however, based on a survey, Proctor (1996) argued convincingly that this rarity is due to behavioral characters not being readily available to the systematists rather than the pervasive notion that behavioral characters are too labial and homoplastic to be reliable. I am reminded of the words of William Sharp MacLeay (1829) in his paper first describing the Mediterranean fruit fly as an agricultural pest and providing its description. To paraphrase: naturalists are the historians of facts, some of which have obvious and immediate utility providing the discoverer with much reward, while others are more obscure. However, when the time comes to evaluate the "noblest branch of our science, the progression of natural affinities," we need all the data we can get — utilitarian or not.

Behaviors used as characters for phylogenetic reconstruction must conform to the criteria applicable to other types of characters used with phylogenetics. The first and foremost criterion is homology. Wenzel's (1992) review of behavioral homology stands as one of the best-organized and most enduring. He suggested that Remane's criteria are useful for postulating behavioral homology and can be translated into behavioral equivalents: morphological position equates to a behavioral sequence; special quality equates to a complex movement in a particular behavioral context; and linkage by intermediate forms is the same as it is for morphology (Wenzel 1992). Wenzel (1992) described many caveats and pitfalls in homologizing behaviors using Remane's criteria, one of which, in particular, is special quality. To use special quality for behaviors, the context in which the behavior occurs must be understood. A broadly defined attribute such as male courtship may be useful for analyzing higher-level taxa, whereas the individual components of male courtship may or may not be homologous depending on the taxonomic level under consideration. Headrick

and Goeden (1994) described a situation that occurs in two distinctive species of tephritines, *Euaresta stigmatica* (Headrick et al. 1995) and *Paracantha gentilis* (Headrick and Goeden 1990). These two species exhibit some of the most complex courtship and mating behavior described for any species of animal, let alone tephritids. Many of the components of the male courtship display are remarkably similar. Are they homologous or homoplasious? If they are homologous, is it because they are borrowed from some other more basic behavior, such as wing displays being derived from flight movements? Even though some of the behavioral elements are different, they function in a similar manner. Thus, is the whole episode of courtship homologous based on function? The complexity of the courtship and mating has no clear adaptive value as neither of these two species cooccurs with any congeners or close relatives. Thus, reproductive isolation is not an adaptive consideration. Wenzel (1992) warned that traits based on function or adaptation should be avoided in phylogeny. Questions regarding homology arise for every behavior. Due to the innate complexity of many behaviors, including "motivation" and learning, systematists are required to develop postulates about homology that include many levels not usually encountered with morphological or molecular characters.

Further, establishing the polarity of behavioral characters is also difficult and compounded by a lack of understanding of the context in which an observed behavior occurs and uniformity of behavioral knowledge among variously allied taxa. There are many identical behaviors that occur in vastly different contexts. A particular wing display may be used by one tephritid species in a clearly defensive maneuver, and in another species as part of a courtship ritual. Again, are the movements (= behavior) homologous or homoplasious? Headrick and Goeden (1994) developed ideas regarding the polarity of larger behavioral groupings: wing displays, wing patterns; pheromone production; territorial displays; and courtship displays. Both pleisomorphic and apomorphic behaviors can be identified in most of these categories. Their rationales for polarity focused mainly on uniqueness in relation to an assumed primitive "root" behavior and the taxonomic ubiquity of the behavior, rather than comparisons with an outgroup. This first attempt is clearly that and requires further study.

On a positive note, Queiroz and Wimberger (1993) showed that behavioral characters are as "sound" as other characters, such as morphological and molecular, in developing phylogenies, or, in other words, they do not exhibit excessive homoplasy. Patterson et al. (1993) discovered that where morphological data and molecular data were available for the same taxa, neither had a greater resolving power over the other where there were highly branching topologies. In her review, Proctor (1996) noted that some authors had determined that behavioral characters produced more parsimonious trees than those generated by morphological data sets. Clearly, the most robust hypothesis regarding phylogeny is one where there is a high level of congruence among independent data sets.

Another point examined by Queiroz and Wimberger (1993) was that most behaviorally derived phylogenies occurred at the species or genus level, rather than for developing relations among higher taxa. Indeed, behaviors have had far more success in the area of taxonomic relationships at the opposite end of the scale — infraspecific taxa. Here behaviors are used to help distinguish between races, biotypes, subspecies, populations, etc. (Bush 1966; 1969; Gordh 1977). Thus, there is enough clarity in a behavioral repertoire to separate intraspecific groupings, but not enough to distinguish higher ranked taxa (Pinto 1977). Proctor (1996) suggested the reason for this pattern is that most behavioral studies focus on taxa that are easily observed and that most behavioral studies do not have taxonomic breadth and relationships as an objective due to logistical and/or time constraints. Headrick and Goeden (1994; and Chapter 25) set out to develop a broad behavioral database for tephritids for eventual use in a phylogenetic context. One of the main problems they encountered was how much behavioral description was needed and what the hierarchy was to be. A similar situation occurs with molecular data, in which the appropriate type of molecular data is matched with the level of taxonomic analysis. Slow changing molecular characters like rDNA work well for higher taxonomic levels; rapidly changing types like mtDNA work well for lower taxa

(Proctor 1996). We are still not sure what types of behavioral data are appropriate to which taxonomic levels in tephritids.

#### 28.4.2.2 Level of Taxonomic Analysis

Behaviors are difficult to describe with accuracy and consistency. Consistency is the key for postulating homology (Headrick and Goeden 1994), and so is context (Wenzel 1992; Proctor 1996). The assumption arises, that once behaviors have been accurately described they can then be homologized. This assumption only scratches the surface of what it means to describe behaviors accurately and in what detail. Headrick and Goeden (1994) attempted to introduce a standardized terminology for tephritid behavioral descriptions with the hope of generating interest in describing behaviors in many different taxa and providing a language to facilitate comparisons — it is still a work in progress. Most behaviors occur as a continuum of movement, one into another, without a clear distinction. The wing displays of tephritids are a case in point. We can describe tephritid wing displays as “extensions,” and under extensions we can have extending one wing at a time or together, and under extending one wing at a time we can have rotating the wing blade while extending the wing or keeping the blade parallel to the substrate. Now we have a hierarchy of behavior. The category of wing extension may be a useful binary character for some higher-level classification within the Tephritoidea, but is certainly far from sufficient to serve for any lower taxonomic evaluation. Farther down the descriptive line we run into problems of a different kind. Variations of a behavioral element do occur among individuals, leading to problems in determining what is a “root” behavior and what is individual embellishment by the performer of the behavior. Too much descriptive detail provides little or no resolving power for a behavioral character. Understanding *how* to describe tephritid behavior is a first step and will require examination of many more species. Headrick and Goeden (1994) have examined approximately 50 species, but they all occur in an evolutionarily advanced group. Examination of the behaviors of other groups, as is currently being done with the more ancestral genera *Blepharoneura* (see Condon and Norrbom, Chapter 7) and *Phytalmia* (Dodson, Chapter 8), is exciting as many behaviors observed in the higher tephritids also occur in these genera.

#### 28.4.2.3 Conclusion

The use of behavioral data to develop new hypotheses of phylogenetic relationships, or to test existing hypotheses, is possible for tephritids. To achieve this we need an intersection, where well-known behavior, well known ecology, and at least a superficial understanding of phylogenetic relationships cross paths. Within our family this crossroads occurs for the genus *Rhagoletis* due to the work of Guy Bush, Ron Prokopy, Stewart Berlocher, Dan Papaj, Jim Smith, and their colleagues, and perhaps this is the best place to start. This genus can serve as a model system to help us determine how detailed our behavioral descriptions should be and at what taxonomic level they will provide the best results. There are many groups within the Tephritidae for which ecology, behavior, or morphology is relatively well known, and it is with these taxa that we can test the hypotheses built from studies on groups such as *Rhagoletis*.

### ACKNOWLEDGMENTS

We are grateful to James Lloyd, Denise Johanowiz, Kevina Vulinec, Naomi Paz, Ora Manheim, and Netta Dorchin for their comments on the manuscript. The writing of this chapter was made possible by the generous financial support of the International Organization for Biological Control of Noxious Animals and Plants (IOBC), the Campaña Nacional contra las Moscas de la Fruta (SAGAR-IICA, Mexico), and USDA-ICD-RSED.

## REFERENCES

- Aldiss, J. 1983. Chemical Communication in British Social Wasps (Hymenoptera: Vespidae). Ph.D. dissertation, University of Southampton, Southampton. 252 pp.
- Aldrich, J.R., J.E. Oliver, W.R. Lusby, J.P. Kochansky, and J.A. Lockwood. 1987. Pheromone strains of the cosmopolitan pest, *Nezara viridula*. *J. Exp. Zool.* 244: 171–175.
- Aldrich, J.A., M.P. Hoffmann, J.P. Kochansky, W.R. Lusby, J.E. Eger, and J.A. Payne. 1991. Identification and attractiveness of a major pheromone component for nearctic *Euschistus* spp. stink bugs (Heteroptera: Pentatomidae). *Environ. Entomol.* 20: 477–483.
- Alexander, R., D. Marshall, and J. Cooley. 1997. Evolutionary perspectives on insect mating. In *Mating Systems in Insects and Arachnids* (J.C. Crespi and B.J. Choe, eds.), pp. 4–41. Cambridge University Press, Cambridge. 387 pp.
- Aluja, M. 1993. Unusual calling behavior of *Anastrepha robusta* (Diptera: Tephritidae) flies in nature. *Fla. Entomol.* 76: 391–395.
- Aluja, M. and A. Birke. 1993. Habitat use by adults of *Anastrepha obliqua* (Diptera: Tephritidae) in a mixed mango and tropical plum orchard. *Ann. Entomol. Soc. Am.* 86: 799–812.
- Aluja, M., M. Cabrera, and J. Hendrichs. 1983. Behavior and interactions between *Anastrepha ludens* (L.) and *A. obliqua* (M.) on a field caged mango tree. I. Lekking behavior and male territoriality. In *Fruit Flies of Economic Importance* (R. Cavalloro, ed.), pp. 122–133. A.A. Balkema, Rotterdam.
- Aluja, M., I. Jácome, A. Birke, N. Lozada, and G. Quintero. 1993. Basic patterns of behavior in wild *Anastrepha striata* (Diptera: Tephritidae) flies under field-cage conditions. *Ann. Entomol. Soc. Am.* 86: 776–793.
- Arakaki, N., H. Kuba, and H. Soemori. 1984. Mating behavior of the oriental fruit fly, *Dacus dorsalis* Hendel (Diptera: Tephritidae). *Appl. Entomol. Zool.* 19: 42–51.
- Arita, L. and K. Kaneshiro. 1983. Pseudomale courtship behavior of the female Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). *Proc. Hawaii. Entomol. Soc.* 24: 205–210.
- Baker, R., R. Herbert, P.E. Howse, and O.T. Jones. 1980. Identification and synthesis of the major sex pheromone of the olive fly (*Dacus oleae*). *J. Chem. Soc. Chem. Commun.* 1: 52–53.
- Barigozzi, C. 1982. *Mechanisms of Speciation*. Alan R. Liss, New York. 546 pp.
- Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2: 349–368.
- Batra, S.W.T. 1979. Reproductive behavior of *Euaestha bella* and *E. festiva* (Diptera: Tephritidae), potential agents for the biological control of adventive North American ragweeds (*Ambrosia* spp.) in Eurasia. *J. N.Y. Entomol. Soc.* 87: 118–125.
- Belford, S.R. and M.D. Jenkins. 1998. Establishing cryptic female choice in animals. *Trends Ecol. Evol.* 13: 216–218.
- Berg, C.O. and K. Valley. 1985. Nuptial feeding in *Sepedon* spp. (Diptera: Sciomyzidae). *Proc. Entomol. Soc. Wash.* 87: 622–633.
- Biggs, J.D. 1972. Aggressive behavior in the adult apple maggot. *Can. Entomol.* 140: 349–353.
- Blum, M.S. 1981. *Chemical Defenses of Arthropods*. Academic Press, New York. 562 pp.
- Bonduriansky, R. 1995. A new Nearctic species of *Protopiophilina* Duda (Diptera: Piophilidae) with notes on its behavior and comparison with *P. latipes* (Meigen). *Can. Entomol.* 127: 859–863.
- Boyce, A.M. 1934. Bionomics of the walnut husk fly *Rhagoletis completa*. *Hilgardia* 8: 363–579.
- Bradbury, J.W. 1981. The evolution of leks. In *Natural Selection and Social Behavior* (R.D. Alexander and D.W. Tinkle, eds.), pp. 138–169. Chiron Press, New York. 532 pp.
- Brittain, W.H. and C.A. Good. 1917. The apple maggot in Nova Scotia. *Bull. Nova Scotia Dep. Agric.* 9: 1–70.
- Brooks, F.E. 1921. Walnut husk fly. *U.S. Dep. Agric. Bull.* No. 992.
- Brown, J.L. and G.H. Orians. 1970. Spacing patterns in mobile animals. *Annu. Rev. Ecol. Syst.* 1: 239–262.
- Burk, T. 1981. Signaling and sex in acalyprate flies. *Fla. Entomol.* 64: 30–43.
- Burk, T. 1982. Evolutionary significance of predation on sexually signaling males. *Fla. Entomol.* 65: 90–104.
- Burk, T. 1983. Behavioral ecology of mating in the Caribbean fruit fly, *Anastrepha suspensa* (Loew). *Fla. Entomol.* 66: 330–344.
- Burk, T. and J.C. Webb. 1983. Effect of male size on calling propensity, song parameters, and mating success in the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 76: 678–682.
- Burkhardt, D. and I. de la Motte. 1988. Big 'antlers' are favoured: female choice in stalk-eyed flies (Diptera, Insecta), field collected harems and laboratory experiments. *J. Comp. Physiol. A Sensory Neural Behav. Physiol.* 162: 649–652.



- Bush, G.L. 1966. The taxonomy, cytology, and evolution of the genus *Rhagoletis* in North America (Diptera: Tephritidae). *Bull. Mus. Comp. Zool.* 134: 431–562.
- Bush, G.L. 1969. Mating behavior, host specificity, and the ecological significance of sibling species in frugivorous flies of the genus *Rhagoletis* (Diptera: Tephritidae). *Am. Nat.* 103: 669–672.
- Cade, W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* 190: 1312–1313.
- Carson, H.L. 1978. Speciation and sexual selection in Hawaiian *Drosophila*. In *Ecological Genetics: The Interface* (P.F. Brussard, ed.), pp. 93–107. Springer-Verlag, New York. 247 pp.
- Cavender, G.L. and R.D. Goeden. 1984. The life history of *Paracantha cultaris* (Coquillett) on wild sunflower, *Helianthus annuus* L. ssp. *lenticularis* (Douglas) Cockerell, in southern California (Diptera: Tephritidae). *Pan-Pac. Entomol.* 60: 213–218.
- Chuman, T., P.J. Landolt, R.R. Heath, and J.H. Tumlinson. 1987. Isolation, identification, and synthesis of male-produced sex pheromone of papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker (Diptera: Tephritidae). *J. Chem. Ecol.* 13: 1979–1992.
- Condon, M.A. and A.L. Norrbom. 1994. Three sympatric species of *Blepharoneura* (Diptera: Tephritidae) on a single species of host (*Gurania spinulosa*, Cucurbitaceae): new species and new taxonomic methods. *Syst. Entomol.* 19: 279–304.
- Cott, H.B. 1940. *Adaptive Coloration in Animals*. Methuen and Co. Ltd., London. 508 pp.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex* (reprinted). Modern Library, New York. 1000 pp.
- Dawkins, R. 1986. *The Blind Watchmaker*. W.W. Norton, New York. 332 pp.
- Dobzhansky, T. 1940. Speciation as a stage in evolutionary divergence. *Am. Nat.* 74: 312–321.
- Dodson, G.N. 1982. Mating and territoriality in wild *Anastrepha suspensa* (Diptera: Tephritidae) in field cages. *J. Ga. Entomol. Soc.* 17: 189–200.
- Dodson, G.N. 1985. Lek mating system and large male aggressive advantage in a gall-forming tephritid fly (Diptera: Tephritidae). *Ethology* 72: 99–108.
- Dodson, G.N. 1987a. The significance of sexual dimorphism in the mating systems of two species of tephritid flies, *Aciurina bigeloviae* and *Valentibulla dodsoni* (Diptera: Tephritidae). *Can. J. Zool.* 65: 194–198.
- Dodson, G.N. 1987b. Biological observations on *Aciurina trixa* and *Valentibulla dodsoni* (Diptera: Tephritidae) in New Mexico. *Ann. Entomol. Soc. Am.* 80: 494–500.
- Dodson, G.N. 1997. Resource defense mating system in antlered flies, *Phytalmia* spp. (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 90: 496–504.
- Downes, J.A. 1969. The swarming and mating flight of Diptera. *Annu. Rev. Entomol.* 14: 271–298.
- Eberhard, W.G. 1994. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. *Evolution* 48: 711–733.
- Eberhard, W.G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton. 504 pp.
- Eberhard, W.G. 1997. Sexual selection by cryptic female choice in insects and arachnids. In *The Evolution of Mating Systems in Insects and Arachnids* (J.C. Choe and B.J. Crespi, eds.), pp. 32–57. Cambridge University Press, Cambridge. 387 pp.
- Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–223.
- Enderlein, G. 1920. Zur Kenntnis tropischer Frucht-Bohrfliegen. *Zool. Jahrb. Abt. Syst. Geogr. Biol. Tiere* 43: 336–360.
- Endler, J.A. and A.L. Basolo. 1998. Sensory ecology, receiver biases, and sexual selection. *Trends Ecol. Evol.* 13: 415–420.
- Féron, M. 1962. *Le Comportement de reproduction chez la mouche méditerranéenne des fruits, Ceratitis capitata* Wied (Dipt. Trypetidae): Comportement sexuel, comportement de ponte. Université de Paris, Paris. 131 pp.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford. 272 pp.
- Fletcher, B.S. 1987. The biology of dactyniine fruit flies. *Annu. Rev. Entomol.* 32: 115–144.
- Fletcher, B.S. and W. Kitching. 1995. Chemistry of fruit flies. *Chem. Rev.* 95: 789–828.
- Foote, B.A. 1967. Biology and immature stages of fruit flies: the genus *Icterica* (Diptera, Tephritidae). *Ann. Entomol. Soc. Am.* 60: 1295–1305.
- Foote, B.A., F.L. Blanc, and A.L. Norrbom. 1993. *Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico*. Comstock Publishing Associates, Ithaca. 571 pp.
- Franke, W., G. Hindorf, and W. Reith. 1979. Alkyl-1,6-dioxaspiro[4,5]decanes. A new class of pheromones. *Naturwissenschaften* 66: 618–619.

- Freidberg, A. 1978. Reproductive behaviour of Fruit Flies. Ph.D. dissertation, Tel Aviv University, Tel Aviv.
- Freidberg, A. 1981. Mating behaviour of *Schistopterum moebiusi* Becker (Diptera: Tephritidae). *Isr. J. Entomol.* 15: 89–95.
- Freidberg, A. 1982. Courtship and post-mating behaviour of the fleabane gall fly, *Spathulina tristis* (Diptera: Tephritidae). *Entomol. Gen.* 7: 273–285.
- Freidberg, A. 1984. The mating behavior of *Asteia elegantula* with biological notes on some other Asteiidae (Diptera). *Entomol. Gen.* 9: 217–224.
- Freidberg, A. 1991. A new species of *Ceratitis* (*Ceratitis*) (Diptera: Tephritidae), key to species of subgenera *Ceratitis* and *Pterandrus*, and record of *Pterandrus* fossil. *Bishop Mus. Occas. Pap.* 31: 166–173.
- Freidberg, A. 1997. Mating trophallaxis in *Metasphenisca negeviana* (Freidberg) (Diptera: Tephritidae). *Isr. J. Entomol.* 31: 199–203.
- Given, B.B. 1953. Evolutionary trends in the Thynninae (Hymenoptera: Tiphidae) with special reference to feeding habits of Australian species. *Trans. R. Entomol. Soc. Lond.* 105: 1–10.
- Goeden, R.D. and D.H. Headrick. 1992. Life history and description of immature stages of *Neaspilota viridescens* Quisenberry (Diptera: Tephritidae) on native Asteraceae in southern California. *Proc. Entomol. Soc. Wash.* 94: 59–77.
- Goeden, R.D., J.A. Teerink, and D.H. Headrick. 1998. Life history and description of immature stages of *Trupanea jonesi* Curran (Diptera: Tephritidae) on native Asteraceae in Southern California. *Proc. Entomol. Soc. Wash.* 100: 126–140.
- Gordh, G. 1977. Biosystematics of natural enemies. In *Biological Control by Augmentation of Natural Enemies* (R.L. Ridgway and S.B. Vinson, eds.), pp. 125–150. Plenum Press, New York.
- Green, T. 1977. A man's obsession reveals the riches of a hidden world. *Smithsonian* 8: 80–86.
- Greene, E., L.J. Orsack, and D.W. Whitman. 1987. A tephritid fly mimics the territorial displays of its jumping spider predators. *Science* 236: 310–312.
- Gwynne, D.T. 1983. Male nutritional investment and the evaluation of sexual differences in Tettigoniidae and other Orthoptera. In *Orthoptera Mating Systems* (D. Gwynne and G. Morris, eds.), pp. 337–366. Westview Press, Boulder.
- Hamilton, W.D. and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218: 384–387.
- Haniotakis, G.E. 1974. Sexual attraction in the olive fruit fly, *Dacus oleae* (Gmelin). *Environ. Entomol.* 3: 82–86.
- Hardy, D.E. 1973. The Fruit Flies (Tephritidae — Diptera) of Thailand and Bordering Countries. *Pac. Insects Monogr.* 31: 353 pp.
- Headrick, D.H. and R.D. Goeden. 1990. Life history of *Paracantha gentilis* (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 83: 776–785.
- Headrick, D.H. and R.D. Goeden. 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. *Stud. Dipterol.* 1: 194–252.
- Headrick, D.H. and R.D. Goeden. 1996. Issues concerning the eradication or establishment and biological control of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), in California. *Biol. Control* 6: 412–421.
- Headrick, D.H., R.D. Goeden, and J.A. Teerink. 1995. Life history and description of immature stages of *Euaesta stigmatica* (Diptera: Tephritidae) on *Ambrosia* spp. (Asteraceae) in southern California. *Ann. Entomol. Soc. Am.* 88: 58–71.
- Heath, R.R. and P.J. Landolt. 1988. The isolation, identification, and synthesis of the alarm pheromone of *Vespula squamosa* (Drury) (Hymenoptera: Vespidae) and associated behavior. *Experientia* 44: 82–83.
- Heath, R.R., P.J. Landolt, J.H. Tumlinson, D.L. Chambers, R.E. Murphy, R.E. Doolittle, B.D. Dueben, J. Sivinski, and C.O. Calkins. 1991. Analysis, synthesis, formulation, and field testing of three major components of male Mediterranean fruit fly pheromone. *J. Chem. Ecol.* 17: 1925–1940.
- Heath, R.R., N. Epsky, B. Dueben, A. Guzman, and L.E. Andrade. 1994. Gamma radiation effects on production of four pheromonal components of male Mediterranean fruit fly (Diptera: Tephritidae). *J. Chem. Ecol.* 17: 1925–1940.
- Hendrichs, J. and M.A. Hendrichs. 1990. Mediterranean fruit flies (Diptera: Tephritidae) in nature: location and diel pattern of feeding and other activities on fruiting and nonfruiting hosts and nonhosts. *Ann. Entomol. Soc. Am.* 83: 632–641.
- Hendrichs, J. and J. Reyes. 1987. Reproductive behavior and post-mating female guarding in the monophagous multivoltine *Dacus longistylus* (Wied.) (Diptera: Tephritidae) in southern Egypt. In *Fruit Flies: Proceedings of the Second International Symposium, 16–21 September 1986, Colymbari, Crete, Greece* (A.P. Economopoulos, ed.), pp. 303–313. Elsevier Science Publishers, Amsterdam.

- Hendrichs, J., Katsoyannos, D. Papaj, and R. Prokopy. 1991. Sex differences in movement between feeding sites and mating sites and tradeoffs between food consumption, mating success, and predatory evasion in Mediterranean fruit flies (Diptera: Tephritidae). *Oecologia* 86: 223–231.
- Hendrichs, J., B.I. Katsoyannos, V. Wornoayporn, and M.A. Hendrichs. 1994. Odour-mediated foraging by yellowjacket wasps (Hymenoptera: Vespidae): predation on leks of pheromone-calling Mediterranean fruit fly males (Diptera: Tephritidae). *Oecologia* 99: 88–94.
- Hendrichs, M.A. and J. Hendrichs. 1998. Perfumed to be killed: interception of Mediterranean fruit fly (Diptera: Tephritidae) sexual signaling by predatory foraging wasps (Hymenoptera: Vespidae). *Ann. Entomol. Soc. Am.* 91: 228–234.
- Höglund, J. and R.V. Alatalo. 1995. *Leks*. Monographs in Behavior and Ecology Series. Princeton University Press, Princeton.
- Iwahashi, O. and T. Majima. 1986. Lek formation and male–male competition in the melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). *Appl. Entomol. Zool.* 21: 70–75.
- Jenkins, J. 1990. Mating behavior of *Aciurina mexicana* (Aczel)(Diptera: Tephritidae). *Proc. Entomol. Soc. Wash.* 92: 66–75.
- Johnston, R.F. 1962. A review of courtship feeding in birds. *Bull. Kans. Ornithol. Soc.* 13: 25–32.
- Kaneshiro, K.Y. 1976. Ethological isolation and phylogeny in the *planitibia* subgroup of Hawaiian *Drosophila*. *Evolution* 30: 740–745.
- Kaneshiro, K.Y. 1980. Sexual selection, speciation, and the direction of evolution. *Evolution* 34: 437–444.
- Kaneshiro, K.Y. 1983. Sexual selection, and direction of evolution in the biosystematics of Hawaiian Drosophilidae. *Annu. Rev. Entomol.* 28: 161–178.
- Kaneshiro, K.Y. 1987. The dynamics of sexual selection and its pleiotropic effects. *Behav. Genetics* 17: 559–569.
- Kaneshiro, K.Y. 1989. The dynamics of sexual selection and founder effects in species formation. In *Genetics, Speciation, and the Founder Principle* (L.V. Giddings, K.Y. Kaneshiro, and W.W. Anderson, eds.), pp. 279–296. Oxford University Press, Oxford. 373 pp.
- Kaneshiro, K.Y. and A.T. Ohta. 1982. The flies fan out. *Nat. Hist.* 91: 54–58.
- Kanmiya, K. 1988. Acoustic studies on the mechanism of sound production in the mating songs of the melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). *J. Ethol.* 6: 143–151.
- Kaston, B.J. 1970. Comparative biology of American black widow spiders. *Trans. San Diego Soc. Nat. Hist.* 16: 34–82.
- Keiser, I., R.M. Kabayashi, D.L. Chambers, and E.L. Schneider. 1973. Relation of sexual dimorphism in the wings, potential stridulation, and illumination to mating of Oriental fruit flies, melon flies, and Mediterranean fruit flies in Hawaii. *Ann. Entomol. Soc. Am.* 66: 937–941.
- Kennedy, B.H. 1979. The effect of multilure on parasites of the European elm bark beetle, *Scolytus multistriatus*. *Bull. Entomol. Soc. Am.* 25: 116–118.
- Kessel, E.L. 1955. The mating activities of balloon flies. *Syst. Zool.* 4: 97–104.
- Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution* 36: 1–2.
- Lambert, D.M. and H.G. Spenser. 1995. *Speciation and the Recognition Concept*. Johns Hopkins University Press, Baltimore. 502 pp.
- Lande, R. 1981. Models of speciation by selection on polyphyletic traits. *Proc. Natl. Acad. Sci. U.S.A.* 78: 3721–3725.
- Lande, R. 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* 36: 213–223.
- Landolt, P.J. 1984. Behavior of the papaya fruit fly *Toxotrypana curvicauda* Gerstaecker (Diptera: Tephritidae), in relation to its host plant, *Carica papaya* L. *Folia Entomol. Mex.* 61: 215–224.
- Landolt, P.J. 1985. Papaya fruit fly eggs and larvae (Diptera: Tephritidae) in field-collected papaya fruit. *Fla. Entomol.* 68: 354–356.
- Landolt, P.J. and J. Hendrichs. 1983. Reproductive behavior of the papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 76: 413–417.
- MacLeay, W.S. 1829. Notice of *Ceratitidis citriferda*, an insect very destructive to orange. *Zool. J.* 4: 475–482.
- Malavasi, A., J.S. Morgante, and R.J. Prokopy. 1983. Distribution and activities of *Anastrepha fraterculus* (Diptera: Tephritidae) flies on host and nonhost trees. *Ann. Entomol. Soc. Am.* 76: 286–292.
- Markow, T.M. and P.F. Ankney. 1984. *Drosophila* males contribute to oogenesis in a multiple mating species. *Science* 224: 302–303.
- Mather, M.H. and B.D. Roitberg. 1987. A sheep in wolf's clothing: tephritid flies mimic spider predators. *Science* 236: 308–310.
- Maynard Smith, J. 1974. The theory of games and the evolution of animal conflict. *J. Theor. Biol.* 47: 209–222.

- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Mayr, E. 1982. Processes of speciation in animals. In *Mechanisms of Speciation* (C. Barigozzi, ed.), pp. 1–19. A.R. Liss, New York. 546 pp.
- Mayr, E. 1963. *Animal Species and Evolution*. Belknap Press of Harvard University, Cambridge. 797 pp.
- McAlpine, D.K. 1979. Agonistic behavior in *Achias australis* (Diptera: Platystomatidae) and the significance of eye stalks. In *Sexual Selection and Reproductive Competition in Insects* (M.S. Blum and N.A. Blum, eds.), pp. 221–230. Academic Press, New York. 463 pp.
- McClintock, W.J. and G.W. Uetz. 1996. Female choice and pre-existing bias: Visual cues during courtship in two *Schizocosa* wolf spiders (Araneae: Lycosidae). *Anim. Behav.* 52: 167–181.
- Metcalf, R.L. 1990. Chemical Ecology of Dacinae fruit flies (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 83: 1017–1030.
- Moffett, M.W. 1997. Flies that fight. *Nat. Geogr.* 192: 68–77.
- Monteith, L.G. 1972. Status of predators of the adult apple maggot, *Rhagoletis pomonella* in Ontario. *Can. Entomol.* 104: 257–262.
- Morgante, J.S., D. Selivon, V.N. Solferini, S.R. Mantioli. 1993. Evolutionary patterns in specialist and generalist species of *Anastrepha*. In *Fruit Flies: Biology and Management* (M. Aluja and P. Liedo, eds.), pp. 15–20. Springer-Verlag, New York.
- Muller, H.J. 1942. Isolating mechanisms, evolution and temperature. *Biol. Symp.* 6: 71–125.
- Munro, H.K. 1949. A remarkable new species of trypetid fly of the genus *Ceratitis* (sensu stricto) from east Africa in the collection of the United States National Museum. *Proc. U.S. Natl. Mus.* 99: 499–501.
- Nation, J.L. 1974. The structure and development of two sex specific glands in the male Caribbean fruit flies. *Ann. Entomol. Soc. Am.* 67: 731–734.
- Norrbom, A.L. and K.C. Kim. 1988. A List of the Reported Host Plants of the Species of *Anastrepha* (Diptera: Tephritidae). USDA-APHIS 81–52.
- Novak, J.A. and B.A. Foote. 1975. Biology and immature stages of fruit flies: the genus *Stenopa* (Diptera, Tephritidae). *J. Kans. Entomol. Soc.* 48: 42–52.
- O'Donald, P. 1977. Theoretical aspects of sexual selection. *Theor. Popul. Biol.* 12: 298–334.
- O'Donald, P. 1980. *Genetic Models of Sexual Selection*. Cambridge University Press, Cambridge. 250p.
- Oldroyd, H. 1964. *The Natural History of Flies*. Weidenfeld and Nicolson, London. 324 pp.
- Otte, D. and J.A. Endler. 1989. *Speciation and Its Consequences*. Sinauer Associates Inc., Sunderland. 679 pp.
- Papaj, D.R. 1994. Oviposition site guarding by male walnut flies and its possible consequences for mating success. *Behav. Ecol. Sociobiol.* 34: 187–195.
- Papaj, D.R., J. Hendrichs, and B.E. Katsovannos. 1989. Use of fruit wounds in oviposition by the Mediterranean fruit fly. *Entomol. Exp. Appl.* 53: 203–209.
- Parker, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. *Cambridge Phil. Soc. Biol. Rev.* 45: 525–567.
- Parker, G.A. 1974. Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* 47: 223–243.
- Parker, G.A. 1978. Evolution of competitive mate searching [insects]. *Annu. Rev. Entomol.* 23: 173–196.
- Parker, G.A. and E.A. Thompson. 1980. Dung fly struggles: a test of the war of attrition. *Behav. Ecol. Sociobiol.* 7: 37–44.
- Persson, P.I. 1976. Description of third instar larval characters in *Spathulina trisitis* (Loew) from Crete (Diptera: Tephritidae). *Entomol. Scand.* 7: 307–308.
- Piersol, W.H. 1907. The curious mating habit of the fly *Rivellia boscai*. *Am. Nat.* 41: 465–467.
- Pinto, J.D. 1977. Comparative sexual behavior in blister beetles of the subtribe Eupomphina (Coleoptera: Meloidae), and an evaluation of its taxonomic significance. *Ann. Entomol. Soc. Am.* 70: 937–951.
- Pritchard, G. 1967. Laboratory observations on the mating behaviour of the island fruit fly *Rioxa pornia* (Diptera: Tephritidae). *J. Aust. Entomol. Soc.* 6: 127–132.
- Pritchard, G. 1969. The ecology of a natural population of Queensland fruit fly *Dacus tryoni* II. The distribution of eggs and its relation to behaviour. *Aust. J. Zool.* 17: 293–311.
- Proctor, H.C. 1996. Behavioral characters and homoplasy: perception vs. practice. In *Homoplasy: The Recurrence of Similarity in Evolution* (M.J. Sanderson and L. Hufford, eds.), pp. 131–152. Academic Press, San Diego.
- Prokopy, R.J. 1976. Feeding, mating, and oviposition activities of *Rhagoletis fausta* flies in nature. *Ann. Entomol. Soc. Am.* 69: 899–904.
- Prokopy, R.J. 1977. Stimuli influencing trophic relations in Tephritidae. *Coll. Int. C.N.R.S.* 265: 305–336.
- Prokopy, R.J. 1980. Mating behavior of frugivorous Tephritidae in nature. *Proc. Symp. Fruit Fly Problems, XVI International Cong. Entomol.*, Kyoto, pp. 37–46.

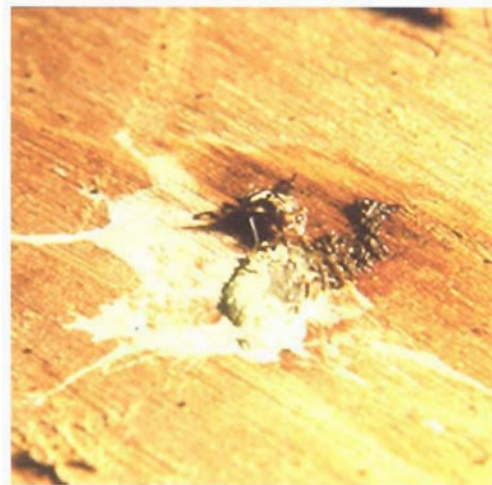
- Prokopy, R.J. and G.L. Bush. 1973. Mating behavior of *Rhagoletis pomonella* (Diptera: Tephritidae) IV. Courtship. *Can. Entomol.* 105: 873–891.
- Prokopy, R.J. and J.J. Duan. 1998. Socially facilitated egg-laying behavior in Mediterranean fruit flies. *Behav. Ecol. Sociobiol.* 42: 117–122.
- Quieroz, A. de and P.H. Wimberger. 1993. The usefulness of behavior for phylogeny estimation: Levels of homoplasy in behavioral and morphological characters. *Evolution* 47: 46–60.
- Quilici, S. and A. Franck. 1997. Field cage studies on mating behavior of *Ceratitidis* spp. (Diptera: Tephritidae) in Reunion Island. 3rd FAO/IAEA Research Coordination meeting on *Medfly Mating Behavior Studies Under Field Cage Conditions*. Tel Aviv, Israel. 11 pp.
- Reichert, S.E. 1998. Game theory and animal contests. In *Game Theory and Animal Behavior* (L.A. Dugatkin and H.K. Reeve, eds.), pp. 64–93. Oxford University Press, New York. 320 pp.
- Roeder, K.D., L. Tozian, and E.A. Weinst. 1960. Endogenous nerve activity and behavior in the mantis and cockroach. *J. Insect Physiol.* 4: 45–62.
- Ryan, M.J. 1998. Sexual selection, receiver biases, and the evolution of sex differences. *Science* 281: 1999–2003.
- Sanderson, M.J., B.G. Baldwin, G. Bharathan, C.S. Campbell, C. Dohlen, D. Ferguson, J.M. Porter, M.F. Wojciechowski, and M.J. Donoghue. 1993. The growth of phylogenetic information and the need for a phylogenetic database. *Syst. Biol.* 42: 562–568.
- Scott, J.P. and E. Fredericson. 1951. The causes of fighting in mice and rats. *Physiol. Zool.* 24: 273–309.
- Shelly, T.E. and T.S. Whittier. 1995. Lek distribution in the Mediterranean fruit fly: influence of tree size, foliage density and neighborhood. *Proc. Hawaii. Entomol. Soc.* 32: 113–121.
- Sigurjónsdóttir, H. and G.A. Parker. 1981. Dung fly struggles: evidence for assessment strategy. *Behav. Ecol. Sociobiol.* 8: 219–230.
- Sivinski, J. 1981. The effects of mating on predation in the stick insect *Diaperomera veliei*. *Ann. Entomol. Soc. Am.* 73: 553–556.
- Sivinski, J. 1989. Lekking and the small-scale distribution of the sexes in the Caribbean fruit fly, *Anastrepha suspensa* (Loew). *J. Insect Behav.* 2: 3–13.
- Sivinski, J. 1997. Ornaments in the Diptera. *Fla. Entomol.* 80: 142–164.
- Sivinski, J. and T. Burk. 1989. Reproductive and mating behavior. In *Fruit Flies: Their Biology, Natural Enemies and Control* (A.S. Robinson and G. Hooper, eds.), pp. 343–351. In *World Crop Pests* (W. Helle, ed.), Vol. 3A. Elsevier Science Publishers, Amsterdam.
- Sivinski, J. and G.N. Dodson. 1992. Sexual dimorphism in *Anastrepha suspensa* (Loew) and other tephritid flies: possible roles of developmental rate, fecundity, and dispersal. *J. Insect Behav.* 5: 491–506.
- Sivinski, J.M. and E. Petersson. 1997. Mate choice and species isolation in swarming insects. In *The Evolution of Mating Systems in Insects and Arachnids* (J.C. Choe and B.J. Crespi, eds.), pp. 294–309. Cambridge University Press, Cambridge. 387 pp.
- Sivinski, J. and B. Smittle. 1987. Male transfer of materials to mates in the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae). *Fla. Entomol.* 70: 233–238.
- Sivinski, J. and J.C. Webb. 1985a. Sound production and reception in the caribfly, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae). *Fla. Entomol.* 68: 273–278.
- Sivinski, J. and J.C. Webb. 1985b. The form and function of acoustic courtship of the papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker (Tephritidae). *Fla. Entomol.* 68: 634–641.
- Sivinski, J. and J.C. Webb. 1986. Changes in a Caribbean fruit fly acoustic signal with social situation (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 79: 146–149.
- Sivinski, J. and J.C. Webb. 1989. Comparisons of acoustic courtship signals in wild and laboratory reared Mediterranean fruit flies, *Ceratitidis capitata*. *Fla. Entomol.* 72: 212–214.
- Sivinski, J., T. Burk, and J.C. Webb. 1984. Acoustic courtship signals in the Caribbean fruit fly, *Anastrepha suspensa* (Loew). *Anim. Behav.* 32: 1011–1016.
- Sivinski, J., N. Epsky, and R. Heath. 1994. Pheromone deposition on leaf territories by male Caribbean fruit flies, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae). *J. Insect Behav.* 7: 43–51.
- Smith, D.C. 1985a. General activity and reproductive behavior of *Rhagoletis cornivora* (Diptera: Tephritidae) flies in nature. *J. N.Y. Entomol. Soc.* 93: 1052–1056.
- Smith, D.C. 1985b. General activity and reproductive behavior of *Rhagoletis tabellaria* (Diptera: Tephritidae) flies in nature. *J. Kans. Entomol. Soc.* 58: 737–739.

- Smith, P.H. 1989. Behavioral partitioning of the day and circadian rhythmicity. In *Fruit Flies: Their Biology, Natural Enemies and Control* (A.S. Robinson and G. Hooper, eds.), pp. 325–341. In *World Crop Pests* (W. Helle, ed.), Vol. 3A. Elsevier Science Publishers, Amsterdam.
- Steck, G.L. 1984. *Chaetostomella undosa* (Diptera: Tephritidae): biology, ecology, and larval description. *Ann. Entomol. Soc. Am.* 77: 669–678.
- Sternlicht, M. 1973. Parasitic wasps attracted by the sex pheromone of their coccid host. *Entomophaga* 18: 339–342.
- Stoltzfus, W.B. and B.A. Foote. 1965. The use of froth masses in courtship of *Eutreta* (Diptera: Tephritidae). *Proc. Entomol. Soc. Wash.* 67: 263–264.
- Teal, P.E.A., J.H. Tumlinson, and R.R. Heath. 1986. Chemical and behavioral analyses of volatile sex pheromone components released by calling *Heliothis virescens* (F.) females (Lepidoptera: Noctuidae). *J. Chem. Ecol.* 12: 107–126.
- Thornhill, R. 1976. Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta: Mecoptera). *Am. Nat.* 110: 529–548.
- Thornhill, R. 1992. Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). *Behav. Ecol.* 3: 277–283.
- Thornhill, R. and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge. 547 pp.
- Trivers, R.L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man* (B. Campbell, ed.), pp. 1871–1971. Aldine, Chicago.
- Turner, M.E. and W.W. Anderson. 1983. Multiple mating and female fitness in *Drosophila pseudoobscura*. *Evolution* 37: 714–723.
- Van der Valk, H. 1987. Spatial and Temporal Dynamics of Mediterranean Fruit Fly, *Ceratitis capitata* Wied. on a Host Tree in the Field. M.S. thesis, Wageningen Agricultural University, The Netherlands.
- Vite, J.P. and D.L. Williamson. 1970. *Thanasimus dubius*: prey perception. *J. Insect Physiol.* 16: 233–239.
- Walker, T.J. 1964. Experimental demonstration of a cat locating orthopteran prey by the prey's calling song. *Fla. Entomol.* 102: 204–208.
- Wallace, A.F. 1869. *The Malay Archipelago*. Dover Press, New York.
- Warburg, M.S. and B. Yuval. 1997. Circadian patterns of feeding and reproductive activities of Mediterranean fruit flies (Diptera: Tephritidae) on various hosts in Israel. *Ann. Entomol. Soc. Am.* 90: 487–495.
- Webb, J.C., J. Sivinski, and C. Litzkow. 1984. Acoustical behavior and sexual success in the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae). *Environ. Entomol.* 13: 650–656.
- Wedell, N. 1994. Variation in nuptial gift quality in bush crickets (Orthoptera: Tettigoniidae). *Behav. Ecol.* 5: 418–425.
- Wenzel, J.W. 1992. Behavioral homology and phylogeny. *Annu. Rev. Ecol. Syst.* 23: 361–382.
- Wheeler, W.M. 1924. Courtship of the Calobatas. *J. Hered.* 15: 485–495.
- White, I.M. 1988. Tephritid Flies (Diptera: Tephritidae). *Handb. Identif. Br. Insects* 10(5a): 134 pp.
- White, I.M. and M.M. Elson-Harris. 1992. *Fruit Flies of Economic Significance: Their Identification and Bionomics*. CAB. International, Wallingford. 601 pp.
- White, M.J.D. 1978. *Modes of Speciation*. Freeman, San Francisco. 455 pp.
- Whitman, D.W., L. Orsack, and E. Greene. 1988. Spider mimicry in fruit flies (Diptera: Tephritidae): further experiments on the deterrence of jumping spiders (Araneae: Salticidae) by *Zonosemata vittigera* (Coquillett). *Ann. Entomol. Soc. Am.* 81: 532–536.
- Whittier, T.S., K. Kaneshiro, and L.D. Prescott. 1992. Mating behavior of Mediterranean fruit flies (Diptera: Tephritidae) in a natural environment. *Ann. Entomol. Soc. Am.* 85: 214–218.
- Wilkinson, G.S. and G. Dodson. 1997. Function and evolution of antlers and eye stalks in flies. In *The Evolution of Mating Systems in Insects and Arachnids* (J.C. Choe and B.J. Crespi, eds), pp. 310–328. Cambridge University Press, Cambridge. 387 pp.
- Wilson, O.E. 1975. *Sociobiology*. Belknap, Cambridge.
- Zahavi, A. and A. Zahavi. 1997. *The Handicap Principle*. Oxford University Press, Oxford. 286 pp.





COLOR FIGURE 1



COLOR FIGURE 2



COLOR FIGURE 3



COLOR FIGURE 4



COLOR FIGURE 5



COLOR FIGURE 6



COLOR FIGURE 7A



COLOR FIGURE 7B



COLOR FIGURE 8



COLOR FIGURE 9

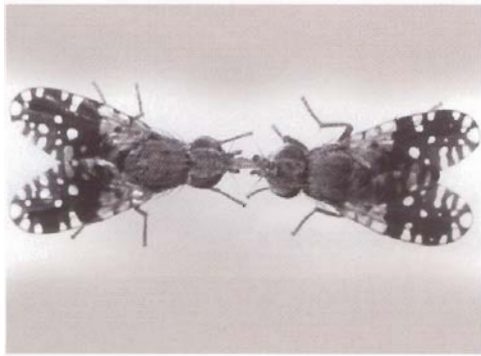


FIGURE 10



COLOR FIGURE 11



COLOR FIGURE 12



COLOR FIGURE 13





COLOR FIGURE 14A



COLOR FIGURE 14B



COLOR FIGURE 14C



COLOR FIGURE 15A



COLOR FIGURE 15B



COLOR FIGURE 15C



COLOR FIGURE 15D



FIGURE 16



COLOR FIGURE 17



COLOR FIGURE 18



COLOR FIGURE 19



COLOR FIGURE 20



COLOR FIGURE 21A



COLOR FIGURE 21B



COLOR FIGURE 21C



COLOR FIGURE 21D

M 3450

# Fruit Flies

(Tephritidae):

Phylogeny  
and Evolution  
of Behavior

Edited by

Martín Aluja, Ph.D.

Allen L. Norrbom, Ph.D.



CRC Press

Boca Raton London New York Washington, D.C.

"Purchased by USDA For  
Official Use"

**Cover Photographs: (Top to Bottom)** (1) Regurgitated droplets deposited by *Anastrepha serpentina* female. These droplets are then reingested by the same female. (Photograph by R. Wilson.) (2) Mating pair of *Anastrepha serpentina*. (Photograph by R. Wilson.) (3) Feeding in damaged guava by females of *Anastrepha ludens* (head in hole) and *A. fraterculus* (entire fly in hole). (Photograph by E. Piedra.) (4) Male of *Ceratitis capitata* releasing pheromone during calling bout. (Photograph by K. Kaneshiro.)

Acquiring Editor: John Sulzyski  
Project Editor: Christine Andreasen  
Cover Design: Dawn Boyd

#### Library of Congress Cataloging-in-Publication Data

Fruit flies (Tephritidae) : phylogeny and evolution of behavior / edited by Martin Aluja and Allen L. Norrbom.

p. cm.

Includes bibliographical references.

ISBN 0-8493-1275-2 (alk. paper)

1. Tephritidae--Phylogeny. 2. Tephritidae--Behavior. I. Aluja, Martin. II. Norrbom, Allen L. (Allen Lee). 1957-  
QL537 T42 F775 1999

595.774--dc21

99-045290

CIP

This work was created in the performance of a Cooperative Research and Development Agreement with the U.S. Department of Agriculture.

This book contains information obtained from authentic and highly regarded sources. Reprinted material is quoted with permission, and sources are indicated. A wide variety of references are listed. Reasonable efforts have been made to publish reliable data and information, but the author and the publisher cannot assume responsibility for the validity of all materials or for the consequences of their use.

Neither this book nor any part may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, microfilming, and recording, or by any information storage or retrieval system, without prior permission in writing from the publisher.

All rights reserved. Authorization to photocopy items for internal or personal use, or the personal or internal use of specific clients, may be granted by CRC Press LLC, provided that \$.50 per page photocopied is paid directly to Copyright Clearance Center, 222 Rosewood Drive, Danvers, MA 01923 USA. The fee code for users of the Transactional Reporting Service is ISBN 0-8493-1275-2/00/\$0.00+\$.50. The fee is subject to change without notice. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

The consent of CRC Press LLC does not extend to copying for general distribution, for promotion, for creating new works, or for resale. Specific permission must be obtained in writing from CRC Press LLC for such copying.

Direct all inquiries to CRC Press LLC, 2000 Corporate Blvd., N.W., Boca Raton, Florida 33431.

**Trademark Notice:** Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation, without intent to infringe.

© 2000 by CRC Press LLC

No claim to original U.S. Government works

International Standard Book Number 0-8493-1275-2

Library of Congress Card Number 99-045290

Printed in the United States of America 1 2 3 4 5 6 7 8 9 0

**Printed on acid-free paper**